SYSTEMATICS AND BIOLOGY OF THE STROMATEID FISHES OF THE GENUS *PEPRILUS*[1]

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ABSTRACT

A complete revision is presented of the genus *Peprilus*, one of the three genera of the family Stromateidae. The nominal genera *Poronotus* and *Palometa* are placed in the synonymy of *Peprilus*. Seven species are recognized, and one, *Peprilus ovatus* from the northern Gulf of California, is newly described.

Several aspects of functional morphology are considered. The vertebral column, skull, and pectoral fins appear to ossify earlier than the caudal skeleton and median fins, a sequence interpreted as being correlated with an early planktonic life followed by an independent nektonic existence. Vertebral number is relatively constant within a species and is considered to be of possible selective value in maintaining a certain body form. The absence of pelvic fins, the long pectoral fins which are used extensively for propulsion in adult fishes, and the compressed body, may all be correlated with the continuous swimming habit of these fishes, especially those larger than 100 mm SL. An hypothesis is proposed that the swimbladder is of hydrostatic advantage to juvenile fishes which hover under jellyfish medusae and that it becomes nonfunctional in larger fishes which swim continuously. The scales are highly deciduous, and the skin is underlain by an extensive canal system, the function of which is unknown. The alimentary canal includes a small mouth with nipping teeth, a toothed, muscular pharyngeal sac which shreds food material, and numerous pyloric caeca and a long intestine which provide a great absorptive area.

Considerations of life history and ecology generally are of four species: *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus*. Spawn-

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ing occurs in the pelagic surface waters at varying distances from shore. The eggs and larvae are planktonic, the latter becoming capable of independent locomotion at a size of about 10 to 15 mm SL. The species occur in a wide range of salinities and variously inhabit all depths over the continental shelf and generally over a sand or mud bottom. The genus is essentially a tropical and warm temperate one with only two species, *P. triacanthus* and *P. simillimus*, reaching cooler waters. Seasonal movements appear to be most pronounced in *P. triacanthus*, the species occurring most abundantly in temperate regions. Fishes smaller than 100 mm SL associate with jellyfish medusae of several genera. This association is apparently important during the early critical growth phases of the fishes. *Peprilus* is a low-level carnivore; jellyfish medusae seem to be an important element in the diet, especially of juveniles. Other food items include a variety of small crustaceans, polychaete worms, and small fishes. Fishes of the genus are evidently significant forage fishes for a number of larger fishes, some of which are of great commercial importance. The economically important species of *Peprilus* are generally taken commercially in a region much smaller than the total range of the species, and this seems to reflect the pattern of migration and center of abundance of the particular species.

Disruption of the Tethys Sea in the Miocene apparently facilitated the segregation of the early members of the family Stromateidae and led to the evolution of the three extant and essentially allopatric stromateid genera. The formation of the Central American land bridge in the Pliocene, the emergence and submergence of land areas associated with the Pleistocene glacial and interglacial periods, and the prevailing current systems all appear to have been important in producing the current level of differentiation and speciation in the genus.

The elongate *P. snyderi* is considered to be the most primitive type, and the deep-bodied *P. paru* the most highly derived form in the genus. The Camin-Sokal method for deducing relationships of contemporaneous species is used to reconstruct a dendrogram of species relationships. Two somewhat subtle species groups are recognized in the genus, and each group is represented on both sides of the Central American isthmus. Character displacement is invoked as a possible mechanism to explain the existence of two apparently distinct populations of *P. triacanthus* in the Atlantic off the southeastern coast of the United States.

The distributions of the species of *Peprilus* appear to correspond generally to the major faunal provinces of the Atlantic Coast and the Pacific Coast of the Americas. The species generally traverse the zoogeographic subdivisions established from the study of small fishes inhabiting rocky shores. Sympatry involves the more diverse species, and the similar or closely related species tend to parallel one another in different oceans or displace one another latitudinally along a continuous coastline. Niche separation seems to be produced largely by spatial arrangement and ecological displacement.

INTRODUCTION

Purpose. One of the main purposes of this study has been to examine specimens of the stromateid genus *Peprilus* from throughout its geographic range, and to determine the limits of the species and the species relationships within the genus. The systematics of the species are considered in the first section of this paper and include a generic description, a key to the species, species descriptions and distributions, and an account of the geographic variation and ontogenetic change. The functional aspects of certain skeletal features, of body form, of the shape, position, and loss of fins, of the integument, and of the alimentary canal are considered in the second section.

Aspects of life history and ecology are considered in the third section and include a general account of the distribution in relation to certain physical factors, of seasonal distribution and abundance, of faunal associations, of larval and juvenile ecology, and of food habits. In this section, the discussion is concentrated on the better known and more accessible species. The final section concerns the evolutionary relationships and zoogeography of the genus and species. The proposed primitive and derived conditions in the genus are discussed, and the Camin-Sokal method is used to reconstruct a dendrogram of probable species relationships. The zoogeographical regions of the North and South American coasts are discussed in relation to the distribution of the species of *Peprilus.* A brief analysis is made of the degree of divergence in allopatric versus sympatric sets of species. The nature and level of speciation in the genus are considered and briefly compared to that of other types of coastal marine fishes.

Background. The fishes of the family Stromateidae comprise a small, well-defined marine group of some 12 to 15 species. Members of this perciform family occur on the continental shelf of oceans of both the Old and New Worlds; none have reached Australia or New Zealand. Haedrich (1967) recognized three genera in the family, *Stromateus, Pampus,* and *Peprilus.* These genera are allopatric except for a small area of overlap between *Stromateus* and *Peprilus* on the east coast of South America, and possibly a similar area on the west coast. *Stromateus* occurs along both coasts of South America, along the West African coast, and in the Mediterranean Sea; *Pampus* occurs from the Iranian Gulf to Japan; and, *Peprilus* is a New World genus of the east and west coasts of North, Central, and northern South America.

Stromateids are small (shorter than 18 inches), essentially pelagic, schooling fishes of coastal regions. Several of the species are commercially important. All possess toothed pharyngeal sacs, a characteristic of the entire suborder Stromateoidei. According to Haedrich (1967), the Stromateidae are the apex in stromateoid evolution.

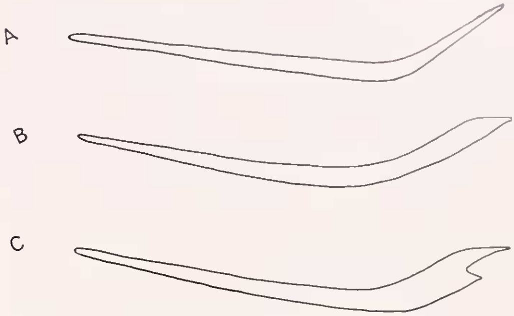

Figure 1. Pelvic bones of the three stromateid genera: A = *Stromateus;* B = *Pampus;* C = *Peprilus.*

The genus *Peprilus* is the most speciose of the family, seven species being recognized in the current study. *Peprilus* is distinguished from the other stromateid genera by the combination of: deep body; large eye; long pectoral fin; two to four small spines ahead of the dorsal and anal fins; a ventral spine on the pelvic bone (Fig. 1); and, no pelvic fins. Differences also exist among the three genera in meristic values; in the number of epural elements in the caudal skeleton (three in one species of *Stromateus,* and two in all other species); and, in the number of branchiostegal rays (five in *Pampus,* six in the other two genera). At least three species of *Peprilus* form important fisheries. The flesh is considered to be of rich and delicate flavor.

Although the stromateid fishes are familiar coastal fishes often collected in large numbers, work on the group has been sporadic; and the relationships within the family have remained enigmatic. Much remains to be known of the life history and distribution of even the most common species. Early revisions of the family include those of Fordice (1884), Jordan and Evermann (1896; 1898), and Regan

(1902). Each of these studies, however, had only limited material available from restricted geographic areas. Haedrich (1967) has provided the most comprehensive and recent revision of the suborder; in his revision he arrived at a classification consisting of five families and fourteen genera. Caldwell (1961) has discussed the populations of one species, *Peprilus triacanthus.*

Studies of the early life history of the Stromateidae, particularly of *Peprilus,* have been largely confined to *P. triacanthus* and, to a lesser extent, *P. paru.* Such works include those of Kuntz and Radcliffe (1918), Hildebrand and Schroeder (1927), Pearson (1941), and Colton and Honey (1963).

Bigelow and Schroeder (1953) reviewed the life history and bionomics of *Peprilus triacanthus* (the butterfish) in the Gulf of Maine. T. J. Hart (1946) discussed at length the bionomics and seasonal distribution of *Stromateus maculatus* (= *S. brasiliensis*) off the Atlantic Coast of South America, and he compared these aspects of the species with those of *Peprilus triacanthus* off the Atlantic Coast of North America. Rege (1958), and Rege and Bal (1964), among others, have contributed to the knowledge of the life history of the species of *Pampus* off the coast of India.

A well-known aspect of the biology of stromateid fishes is their association with coelenterates, either medusae or siphonophores, in the pelagic environment. Mansueti (1963) has reviewed the literature on this association and has provided additional information on the interaction between *Peprilus paru* and the scyphomedusa, *Chrysaora quinquecirrha.* Stromateoids are also known to hover beneath flotsam and *Sargassum* weed (Besednov, 1960; Gooding and Magnuson, 1967). The hovering of stromateids beneath floating objects has not been well documented but probably does occur.

Kennedy and Milkman (1956) demonstrated that the lens of the butterfish, *Peprilus triacanthus,* transmits a considerable band of ultraviolet (UV) light. They indicated that a plankton-feeding fish, for example, might use UV sensitivity to locate areas of suspended matter, including organisms, by responding to the light of shortwave length scattered from such particles. Such a mechanism may facilitate the search for food or the location of jellyfish medusae.

Morphological and anatomical studies of stromateoid fishes are few. Haedrich's (1967) comparative study of the osteology of the group, and Bühler's (1930) extensive account of the digestive tract of the Centrolophidae and Stromateidae, are among the most notable contributions in this area. Gilchrist (1922) examined the teeth of the pharyngeal sac of stromateoids of South Africa, and Barnard (1948) revised and extended the former's work. Isokawa *et al.* (1965) have made additional contributions to the study of pharyngeal sacs and teeth.

Fossil stromateoids are few. Two new fossil genera have been found by Bonde (1966) in the lower Eocene of Denmark. However, no discoveries to date can be reliably referred to the Stromateidae.

Since the three stromateid genera are essentially allopatric, it is reasonable to treat each genus separately. This study is primarily concerned with the genus *Peprilus,* although reference to, and comparison with, other stromateids and other members of the suborder are made.

Three species of *Peprilus, P. paru, P. triacanthus,* and *P. simillimus,* are familiar fishes of North American coasts, but other members of the genus are less well known. Currently in fishery and faunal works, three genera are frequently recognized within what is here considered the genus *Peprilus.* The characters used for generic separation seem more reasonably to be criteria for delineating species; the species form a reasonably compact group. There are close species pairs in the genus, and there has been doubt as to whether certain populations constitute valid species. Active speciation is in the process and creates uncertainty as to rank.

MATERIALS AND METHODS

The list of specimens examined for each species is included in the systematic section under the particular species in alphabetical order of museum and institutional names. Museum and institutional names are abbreviated as follows:

ANSP — Academy of Natural Sciences of Philadelphia
BM — Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
BC — University of British Columbia, Vancouver
CAS — California Academy of Sciences, San Francisco
FMNH — Field Museum of Natural History, Chicago
FSBC — Florida Board of Conservation Marine Laboratory, St. Petersburg
IMS — University of Texas Marine Science Institute at Port Aransas
LACM — Los Angeles County Museum
MCZ — Museum of Comparative Zoology, Harvard University
SIO — Scripps Institution of Oceanography, La Jolla
SU — Division of Systematic Biology, Stanford University
TABL — U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami
TU — Tulane University, New Orleans
USNM — United States National Museum, Washington, D.C.
UCLA — University of California, Los Angeles
UMML — Institute of Marine Sciences, University of Miami
UW — University of Washington, Seattle
WHOI[1] — Woods Hole Oceanographic Institution

Distributional and ecological data were obtained from three Bureau of Commercial Fisheries laboratories: Biological Laboratory, Woods Hole, Massachusetts; Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi; and, Fishery-Oceanography Center, La Jolla, California. Certain data on larval fishes were obtained from the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia.

Two lots of specimens collected on Cruise 16 of the R/V ANTON BRUUN were received from the Smithsonian Oceanographic Sorting Center, Washington, and are listed as uncatalogued specimens of *Peprilus medius* in the MCZ.

Three lots of specimens, two of *Peprilus burti* and one of *P. paru,* were collected personally at Port Aransas, Texas, and are listed as uncatalogued specimens in the MCZ.

Measurements were made point-to-point to the nearest tenth millimeter with a pair of fine point dial calipers. A dissecting microscope was used in measuring very small specimens.

Measurements made were: total length (TL); standard length (SL); head length; snout length; eye diameter; length of upper jaw; interorbital width; length of pectoral fin; predorsal distance I; predorsal distance II; preanal distance; maximum depth of body; and, least depth of caudal peduncle.

Counts in all but the largest specimens were made using a fine needle and under low magnification. Median fin-ray counts of very small specimens were made using transmitted, polarized light.

Counts made were: total dorsal fin elements (D); total anal fin elements (A); total pectoral fin elements (P); total gill rakers; precaudal and caudal vertebrae; and, lateral line scales.

Except for predorsal distances I and II, all measurements and counts conform to the methods of Haedrich (1967). Predorsal distance I is the distance from the tip of the snout to the base of the first element of the dorsal fin. Predorsal distance II is the distance from the tip of the snout to the anterior edge of the first free interneural.

Skeletal features were studied from radiographs and cleared-and-stained specimens. Radiographs suitable for counting vertebrae and for general osteological examination were made with three differ-

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[1] These specimens will ultimately be deposited in the MCZ.

TABLE 1. NUMBER* OF DORSAL FIN-RAYS IN SPECIES OF *PEPRILUS*.

SPECIES	38	39	40	41	42	43	44	45	46	47	48	49	50	51
medius					1	1	7	33	40	34	33	7		2
ovatus			11	10	33	52	22	12	5					
simillimus				1	7	13	15	31	15	13	3			
snyderi						1		4	7	6	4	2		
burti	1	2	2	5	14	55	30	31	12	2	1			
triacanthus			4	5	7	25	30	53	15	7	4			
paru	1	2	8	23	29	59	23	25	5	3				

* Excluding spines.

ent types of industrial X-ray film at settings of 30 kilovolts and 200 milliampere-seconds or of 50–54 kilovolts and 100–150 milliampere-seconds, depending upon the type of film and size of specimens. The enzyme method of clearing-and-staining small vertebrates developed by W. R. Taylor (1967) was used exclusively in this study. Specimens ranging in size from six to 115 mm SL were successfully prepared using this method.

Drawings of each species were made from actual specimens with the aid of radiographs. Other drawings were made similarly, but with the aid of a camera lucida attached to a Wild dissecting microscope. The drawing of the digestive tract is semi-diagrammatic although made from a specific preparation.

Size-on-size and ratio-on-size diagrams are used for each species to show changes with growth and to make species comparisons.

Five characters, head length, eye diameter, body depth, length of pectoral fin, and depth of caudal peduncle, each expressed as a percentage of standard length, were plotted on standard length. The resulting scatter diagrams show trends and indicate change in size of body parts relative to standard length, but because of the wide scatter and curvilinearity, straight lines were not fitted to the data. Parr (1956) has advocated the use of ratio-on-size diagrams in preference to size-on-size diagrams. Ratios, however, have a greater inherent error than the measurements of which they are composed and are to be used cautiously (Simpson, Roe, and Lewontin, 1960: 18; Sokal, 1965: 346).

Five characters, eye diameter, length of upper jaw, length of pectoral fin, body depth, and depth of caudal peduncle, each expressed as a direct value, were plotted on standard length. Straight lines ($Y = A + BX$) were fitted to these size-on-size diagrams without transformation of the values by the method described by Bartlett (1949) and outlined by Simpson *et al.* (1960: 232). The regression lines for each character are presented in a single diagram for all the species, and the statistics of the lines are tabulated.

Measurements of either 24, 90, or 100 specimens were used for the size-on-size diagrams and of either 24, 90, or 109 specimens for the ratio-on-size diagrams. The specimens were randomly chosen from the broadest size and geographical ranges possible. Except for the few additional specimens used in certain of the ratio-on-size plots, measurements of the same specimens were used for both types of diagrams.

Computation of statistics describing the size-on-size regressions was performed at the Harvard Computation Laboratory on an IBM 7094 digital computer.

Unless indicated otherwise, other statistical procedures follow methods described by Simpson *et al.* (1960).

SYSTEMATICS

Genus *Peprilus* Cuvier, 1829

Rhombus Lacépède, 1800: 60. (Type species: *Chaetodon alepidotus* Linnaeus, 1766: 460, by monotypy. Charleston, South Carolina. Pre-

TABLE 2. NUMBER* OF ANAL FIN-RAYS IN SPECIES OF *PEPRILUS*.

SPECIES	35	36	37	38	39	40	41	42	43	44	45	46	47
medius						1	2	17	44	41	32	16	4
ovatus						7	14	29	50	20	20	6	
simillimus	1		6	15	30	28	12	5	2	1			
snyderi						3	8	1	7	4			
burti	1	1	4	15	51	43	26	11	3				
triacanthus			2	10	33	40	34	23	9	1			
paru	1	2	7	20	32	29	31	30	18	4	2		

* Excluding spines.

occupied by *Rhombus* Humphrey, 1797, Mollusca.)

Peprilus Cuvier, 1829: 213. (Type species: *Sternoptyx gardenii* Bloch and Schneider, 1801: 494; by subsequent designation of Gill, 1862: 126. Charleston, South Carolina. A synonym of *Chaetodon alepidotus* Linnaeus, 1766: 460.)

Poronotus Gill, 1861: 35. (Type species: *Stromateus triacanthus* Peck, 1804: 48, fig. 2, pl. II, by monotypy. Piscataqua River, New Hampshire.)

Palometa Jordan and Evermann, 1896: 966. (Subgenus. Type species: *Stromateus palometa* Jordan and Bollman, 1889: 156, by original designation. Elevated to generic rank, Jordan and Evermann, 1898: 2849. Panama Bay, Pacific Ocean.)

Simobrama Fowler, 1944: 2, fig. 2. (Type species: *Seserinus xanthurus* Quoy and Gaimard, 1824: 384, by original designation. Rio de Janeiro, Brazil. A synonym of *Stromateus paru* Linnaeus, 1758: 248.)

Diagnosis. The genus *Peprilus* is distinguished from other stromateid genera by the combination of deep body, large eye, long pectoral fin, two to four bladelike spines anterior to the rays of the dorsal and anal fins, a ventral spine on the pelvic bone, and no pelvic fins. Also, *Peprilus* is distinguished specifically from the stromateid genus *Pampus* in having six rather than five branchiostegal rays and in having a movable rather than a fixed maxillary bone. *Peprilus* is further distinguished from *Stromateus* in having 29 to 36 vertebrae rather than approximately 42 to 48.

Description. Body deep, ovate to elongate, depth 35 to 87 per cent of standard length, highly compressed. Caudal peduncle short, slender, and compressed. Dorsal and ventral profiles convex and similar; anterior dorsal profile slightly to strongly convex. Snout short and blunt; jaws equal; maxilla just reaching to line of anterior margin of eye; eye large with surrounding adipose tissue reaching to nostrils; eye diameter either as great or greater than length of snout. Nostrils double, anterior round, posterior a slit, directly anterior to eye, near end of snout. Dorsal and anal fins with long base, similar to each other, either slightly, moderately, or extremely falcate, as produced by elongation of the first 10 to 13 rays; dorsal and anal coterminal just anterior to caudal peduncle. Dorsal fin with two to four small, bladelike spines anterior to and continuous with 40 to 51 fin-rays; spines often irregular in shape, free surface jagged or crenulated, anterior spine pointed on both ends; third or fourth spine often difficult to distinguish from anteriormost rays. Anal fin equal to or shorter than dorsal, with two or three (rarely four) small spines preceding and continuous with the 35 to 47 fin-rays; spines usually easier to distinguish than in dorsal since rays of anal are more distinctly segmented. Pectoral fin lateral,

TABLE 3. NUMBER OF PECTORAL FIN-RAYS IN SPECIES OF *PEPRILUS*.

SPECIES	17	18	19	20	21	22	23	24
medius				2	10	52	75	19
ovatus			1	9	74	54	12	
simillimus			1	15	65	25	1	
snyderi					3	10	9	
burti			2	16	60	65	5	
triacanthus	1	1	4	51	71	21		
paru		1	1	17	39	63	40	11

TABLE 4. TOTAL NUMBER OF GILL RAKERS IN SPECIES OF *PEPRILUS*.

SPECIES	20	21	22	23	24	25	26	27
medius				15	47	67	24	1
ovatus		2	7	56	63	17	1	
simillimus				19	29	19	8	
snyderi				6	6	4	2	
burti		1	14	26	26	3	1	
triacanthus			4	8	10	11		
paru	9	39	44	6				

just below level of eye, long, winglike, lower rays much shorter than upper ones, base of fin slightly inclined, becoming relatively longer with age, often short and fanlike in larvae and small juveniles; 17 to 24 rays. No pelvic fins, a small spine on the posterior end of the fused pelvic bones projects posteroventrally through the skin at mid-ventral line below base of pectoral fin; pelvic bones closely adjacent anteriorly, fused posteriorly. Edge of coracoid may project underneath head at level of preopercular margin. Caudal fin long to very long, deeply forked, about 18 to 40 per cent of total length; lobes equal. Scales small, cycloid, irregular in shape, deciduous; occasionally with small, blunt, knoblike structures on posterior surface; scales often crowded, usually absent in preserved material; cheek, suborbital area, preopercle, and sometimes opercle scaled; top of head and nape generally scaleless; scales extending onto caudal, dorsal, and anal fins, less so on pectorals, usually only to base of latter. Lateral line of trunk of simple, tubed scales which are often less deciduous than those of rest of body; lateral line above intermuscular septum, either following dorsal profile or more highly arched anteriorly, extending from cleithrum onto caudal peduncle to base of caudal fin. A branch of lateral line extends from immediately above eye posteriorly to head of hyomandibula where it joins a similar branch then turns upward toward mid-dorsal line in a wide, bony tract; cephalic lateral line of pores and branching canals on cheek, opercular area, snout, lower jaw, and top of head. Subdermal canal system on body, top of head and nape; main canal along intermuscular septum with numerous, parallel side-branches; often only partially visible or completely invisible in preserved material. Skin of top of head underlain by a series of small, dendritic canals extending backward over nape. In two species there is an irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. A third species often has a series of slightly smaller, irregularly-spaced pores along entire dorsal surface. All species have very small pores scattered over body, apparently in association with the subdermal canal system. Head about 25 to 40 per cent of standard length, depending upon species and age. Premaxilla not protractile; maxilla movable. Lacrimal bone small, end of maxilla exposed when mouth closed. No supramaxilla. Jaw teeth small, uniserial, close-set; premaxillary teeth slightly recurved, either pointed and simple, or, in two species, with three small cusps; in at least

TABLE 5. NUMBER OF VERTEBRAE IN SPECIES OF *PEPRILUS*.

	PRECAUDAL				CAUDAL						
SPECIES	12	13	14	15	16	17	18	19	20	21	22
medius		173	8						20	153	8
ovatus	3	154					5	143	9		
simillimus		158	2			138	22				
snyderi			3	20						20	3
burti		273			5	262	6				
triacanthus		279				7	62	208	2		
paru	1	181			3	176	3				

two other species both types of premaxillary teeth may be present; teeth of lower jaw with three to five small cusps; slightly more closely spaced than premaxillary teeth. Vomer, palatines, and basibranchials toothless. Gill membranes united across isthmus, divided from about level of anterior part of eye. Opercle and preopercle thin, flat; preopercle finely striated; opercular margins entirely with two flat, blunt, ill-defined spines. Gill rakers similar in all species, slightly more than one-half the length of filaments; with fine teeth on inner edge; closely set; six to nine on epibranchial, one at junction of elements, and 13 to 18 on lower elements of first arch (cerato- and hypobranchials). Pseudobranch small. Six branchiostegal rays, four on ceratohyal, two on epihyal. Vertebrae, 12 to 15 precaudal, 16 to 22 caudal, 29 to 36 total. Three free interneural bones anterior to dorsal fin. Sclerotic bones well ossified. Toothed pharyngeal sac behind last gillarch as in all other stromateoid fishes, joining tubular esophagus; stomach a simple sac; intestine long and in loops, about two and one-half to three times the standard length of the body; pyloric caeca numerous, short, in a dendritic mass adjacent to stomach. Swimbladder thin-walled, physoclistous, continuous with dorsal peritoneum; easily deflated; possibly nonfunctional or absent in adults; found only in fish smaller than 80 to 100 mm SL; not yet seen in all species. Buccal and pharyngeal cavities light in color; peritoneum silvery, with peppering of black pigment that is more dense dorsally. Gonads paired, in posteroventral region of body cavity; ovary in mature and maturing specimens elongate, yellow, and granular; eggs in ripe ovary spherical, yellowish, less than 1 mm in diameter; testis in mature and maturing individuals elongate, thin, yellowish white, and smooth in texture. No external sexual dimorphism apparent.

Color in life iridescent bluish or greenish silver dorsally to silver ventrally. At least one species often has large, dark spots on the dorsal and upper ventral surface. Color in preservative varying from bluish brown to brown dorsally to silver ventrally or body completely brown or bluish brown. Individual melanophores conspicuous in specimens up to about 80 to 100 mm SL, dense and small dorsally, larger and more dispersed ventrally. Anal and dorsal fins with distinct melanophores on membranes between fin-rays, slightly less evident on the paler caudal and pectoral fins. Eye usually darker than rest of body, lens opaque surrounded by iris which is either completely black or partly black and partly yellowish white.

Key to the Species of *Peprilus*

Ranges of proportional measurements in thousandths of standard length and ranges of meristic values are each followed by the mean or two different means (when for two species) in parentheses.

1a. Row of about 17 to 25 relatively large pores immediately below anterior half of dorsal fin; premaxillary teeth usually with three small cusps 2

1b. No row of pores below anterior half of dorsal fin; premaxillary teeth pointed, simple 3

2a. Body elongate, shallow to moderately deep 364 to 600 ($\bar{x}$ 458); eye moderately large, 061 to 133 (086); caudal vertebrae 17 to 20, usually 19, rarely 17 or 20; dorsal and upper ventral surface in adults often mottled with dark spots .... *P. triacanthus* (Peck, 1804) p. 197, Figs. 21, 22.

2b. Body moderately elongate, moderately deep to deep, 460 to 640 ($\bar{x}$ 551); eye large, 065 to 144 (100); caudal vertebrae 16 to 18, usually 17; dorsal or upper ventral surface rarely if ever mottled .... *P. burti* Fowler, 1944 p. 192, Fig. 19.

3a. Dorsal and anal fins except in larvae and juveniles smaller than 50 to 75 mm SL moderately to extremely falcate, the longest anal ray six or more times the length of the shortest anal ray; dorsal often slightly less falcate 4

3b. Dorsal and anal fins only slightly falcate, the longest dorsal and anal rays less than six times the length of the shortest of each 5

4a. Body ovate, very deep, 565 to 877 ($\bar{x}$ 710); dorsal rays 38 to 47, usually 41 to 45 (42.9); gill rakers 20 to 23, usually 21 or 22 (21.5); caudal vertebrae 16 to 18, usually 17 ....

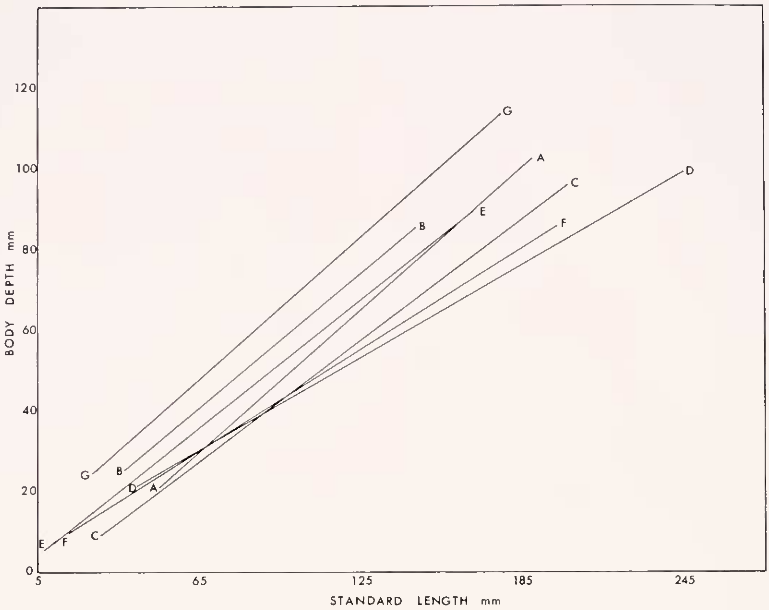


Figure 2. Regression of body depth on standard length for each species of *Peprilus*: A = *P. medius*; B = *P. ovatus*; C = *P. simillimus*; D = *P. snyderi*; E = *P. burti*; F = *P. triacanthus*; G = *P. paru*. Statistics in Table 6.

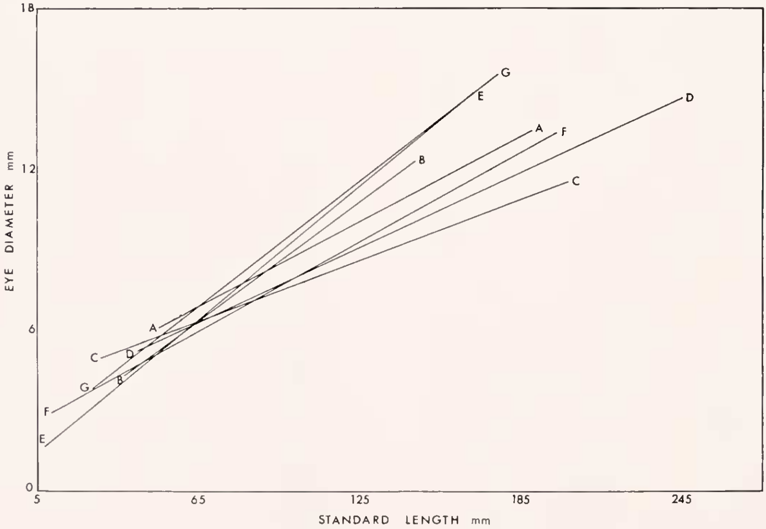


Figure 3. Regression of eye diameter on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

.... *P. paru* (Linnaeus, 1758) p. 202, Fig. 24.

4b. Body moderately elongate, moderately deep to deep, 459 to 618 (x̄ 529); dorsal rays 42 to 51, usually 45 to 48 (46.7); gill rakers 23 to 27, usually 24 to 26 (24.7); caudal vertebrae 20 to 22, usually 21 .... *P. medius* (Peters, 1869) p. 175, Fig. 8.

5a. Body ovate, deep, 542 to 676 (x̄ 619); eye moderately large, 078 to 115 (093); snout length considerably less than eye diameter, 052 to 074 (063); dorsal spines 3 or 4, most frequently 4; often a series of irregularly-spaced, medium-sized pores visible along dorsal surface; total vertebrae 31 to 33, usually 32 (32.0) .... *P. ovatus* sp. n., p. 182, Fig. 10.

5b. Body elongate, shallow to moderately deep, 371 to 517 (x̄ 427, 461); eye small, 050 to 119 (070, 073); snout length about equal to eye diameter, 058 to 083 (068, 070); dorsal spines 2 to 4, usually 3; no series of medium-sized pores usually visible along dorsal surface; total vertebrae 30, 31, or 36 6

6a. Dorsal rays 43 to 49, usually 45 to 48 (x̄ 46.5); anal rays 40 to 44 (42.0); caudal vertebrae 21 or 22, usually 21; total vertebrae 36 .... *P. snyderi* Gilbert and Starks, 1904 p. 189, Fig. 16.

6b. Dorsal rays 41 to 48, usually 43 to 47 (x̄ 44.8); anal rays 35 to 44, usually 38 to 41 (39.5); caudal vertebrae 17 or 18, usually 17; total vertebrae 30 or 31 .... *P. simillimus* (Ayres, 1860) p. 185, Fig. 13.

Peprilus medius (Peters, 1869)

Figures 8, 18a

Stromateus medius Peters, 1869: 707 (original description, Mazatlán, México, holotype seen, 138.4 mm SL, BM 7073); Jordan, 1883: 284; Fordice, 1884: 314.

Stromateus palometa Jordan and Bollman, 1889: 156 (original description, Pacific Ocean, off coast of Panama, 8°16′30″N, 79°37′45″W, ALBATROSS 2804, holotype not seen; four paratypes seen, 50.0 to 58.3 mm SL, SU 434).

Rhombus (*Palometa*) *palometa*, Jordan and Evermann, 1896: 966, *Palometa* erected as subgenus.

Rhombus (*Palometa*) *medius*, Jordan and Evermann, 1896: 967.

Palometa palometa, Jordan and Evermann, 1898: 2849, subgenus *Palometa* elevated to generic level; Jordan, Evermann, and Clark, 1930: 267.

Palometa media, Jordan and Evermann, 1898: 2849; Jordan, Evermann, and Clark, 1930: 267.

Peprilus palometa, Gilbert and Starks, 1904: 85; Meek and S. F. Hildebrand, 1925: 412; Haedrich, 1967: 107.

Peprilus medius, Gilbert and Starks, 1904: 88; Meek and S. F. Hildebrand, 1925: 413; Haedrich, 1967: 107.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BM 7073 (1:138.4 mm, holotype of *Stromateus medius* Peters, Mazatlán, Mexico); BC 56–164 (1:113.0, Paita, Peru, CS); *BC 56–233 (5:143.7–186.0, Paita, Peru); *BC 59–668 (28:108.6–144.0, Pacific Ocean, Panama Bay near Panama City); *BC 59–685 (6:119.3–139.5, Pacific Ocean, Chiman area SE of Panama City); *BC 59–686 (3:125.7–139.6, Pacific Ocean, near Puerto Obaldia, Panama); *BC 59–687 (4:124.8–174.0, Panama City market); *BC 60–25 (1:143.5, Mexico, Golfo de Tehuantepec, Puerto Arista to Salina Cruz); *BC 60–115 (2: 37.4, 144.5, Pacific Ocean, Taboga I., off Panama); BC 61–126 (1:189.0, Mex., Acapulca market); *BC 61–151 (1:131.0, Mazatlán, Mex.); *FMNH 20500 to 20503 (4:123.5–158.5, Panama City market, February-March, 1911); *FMNH 73840 (8: 109.6–185.0, Mex., 1–5 miles off Chiapas coast at Guatemala border to above San Benito, 18–27 m, 14–18 December 1954, 5 radiographed); *LACM 6545–2 (1:112.9, Sinaloa, Mex., 30 August 1962); *LACM 6917–8 (1:163.2, Pacific Ocean, El Savador, Fondo del Mar, August, 1965); *MCZ uncat. (15:111.2–140.6, R/V ANTON BRUUN Cr. 16, Sta. 624E, 04°53′S, 81°23′ W, 75–91 m, 2 June 1966, 14 radiographed); *MCZ uncat. (11:75.3–90.8, R/V ANTON BRUUN Cr. 16, Sta. 624b, 04°48′S, 81°17′W, 16 m, 2 June 1966, 1 CS); *SIO H51–324 (1:141.3, Golfo de Fonseca, Honduras, about 13°00′N, 87°40′ W, 1 August 1951, M/V RENOWN); *SIO 55–58 (1:130.5, Pacific Ocean, between San Diego, California, and Ecuador, dipnet from tuna clipper, July, 1955); *SIO 59–263 (5:76.5–80.5, Sinaloa, Mex., off Rio San

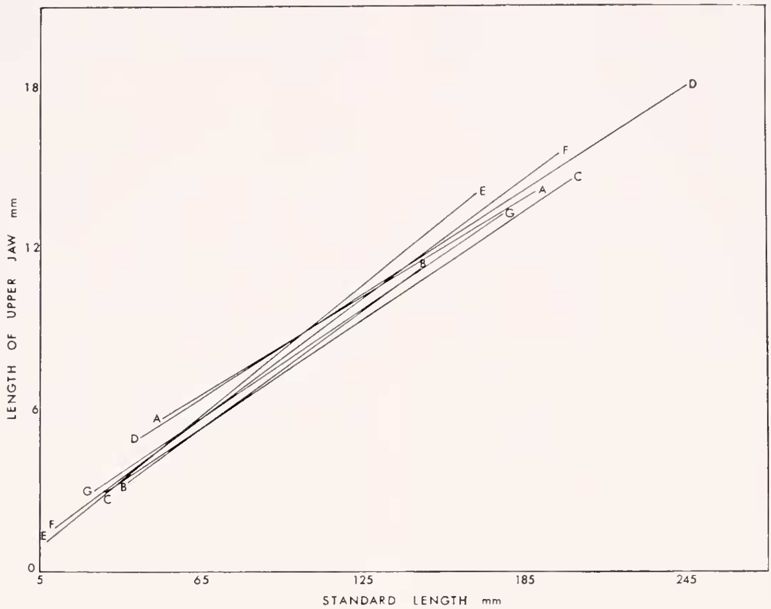


Figure 4. Regression of length of upper jaw on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

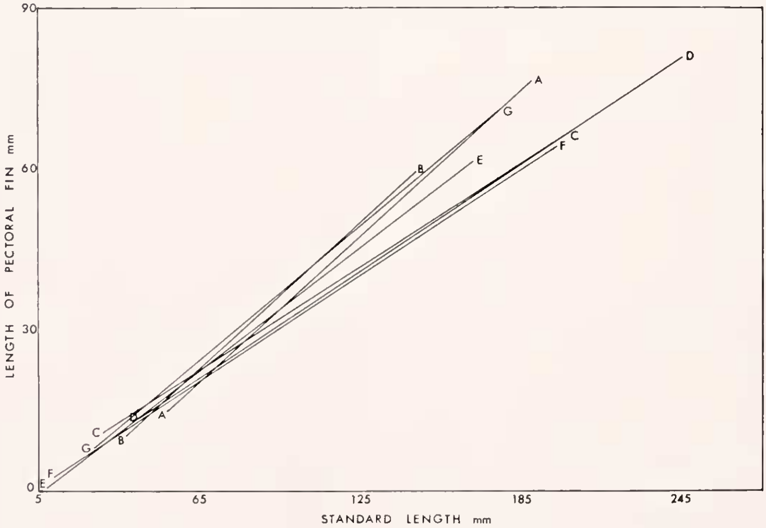


Figure 5. Regression of length of pectoral fin on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

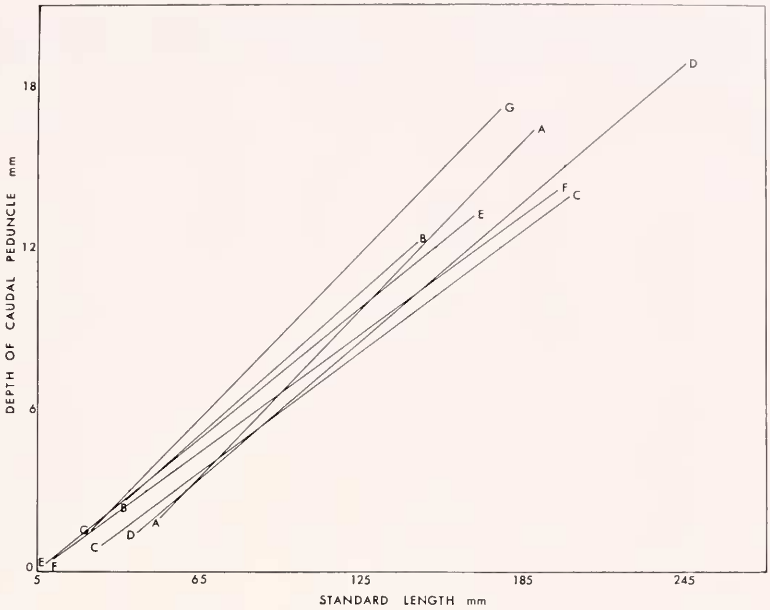


Figure 6. Regression of depth of caudal peduncle on standard length for each species of *Peprilus*. Symbols as in Figure 2. Statistics in Table 6.

Lorenzo, 23°50.5′N, 107°18.2′W, 77–88 m, 16 May 1959, SIO Vermilion Sea Expedition, 4 radiographed; *SIO 64–749 (1:112.4, Panama, off San Carlos, 17 August 1961); *SU 434 (4:50.0–58.3, paratypes of *Stromateus palometa* Jordan and Bollman, 1889, off coast of Panama, ″N, 79°8°16′3037′45″′W, ALBATROSS Sta. 2804, 86 m); *SU 1867 (1:68.0, same as SU 434 above, part of type material of *Stromateus palometa,* incorrectly labeled as From Galapagos Is., according to S. F. Hildebrand (MS)); *SU 6998 (5:136.0–180.4, Panama); *USNM 41272 (1:65.0, Pacific Ocean, ALBATROSS Sta. ?); *USNM 200351 (1:150.0, Peru, Caleta Cruz, Tumbes, 37–55 m, 25 March 1965); *UCLA W51–246 (2:140.0, 146.5, Ecuador, vicinity of Guayaquil, 16 November 1951); *UCLA W53–275 (19:110.6–178.0, Panama Bay between Panama city and Punta Gorda, 4–27 m, 1–5 July 1953); UCLA W53–311 (2: 109.7, 111.8, Panama, between Islas Perlas and Isla Otogne, 8°32′10″N, 79°21′11″W, 64 m, 19 March 1953); *UCLA W54–55 (1:121.3, Costa Rica, S of Golfo de Nicoya, 9–27 m, 29 November 1952); *UCLA W54–167 (1:141.2, Costa Rica, Golfo de Nicoya, 5–8 m, 16–18 April 1952); *UCLA W54–334 (6:121.8–163.5, Panama Bay, mouth of Anton River, 15 m, 21 May 1954); *UCLA W56–112 (2:111.1, 112.5, Gulf of California, Sinaloa, Mex., Bahía Topolobampo, from mouth to 6–9 miles N, 2–9 m, 22 May 1956); *UCLA W56–113 (15:84.5–115.4, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, 6–11 m, 24 May 1956); *UCLA W56–115 (1:96.0, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, in main channel from islands E of town to Punta Copas, 13 m, 31 May 1956); *UCLA W56–117 (11:84.7–108.2, Gulf of Calif., Sinaloa, Mex., Bahía Topolobampo, N of entrance, 9–13 m, June, 1956); *UCLA W56–123 (2:109.6, 112.2, Gulf of Calif., Sinaloa, Mex., vicinity of I. de Altamura, 25°15′N, 108°30′W, 9 m, 10 March 1956); *UCLA W58–46 (1:163.8, Gulf of Calif.,

TABLE 6. STATISTICS DESCRIBING REGRESSIONS ($y = a + bx$) OF BODY MEASUREMENTS ON STANDARD LENGTH, FIGS. 2–6, FOR THE SPECIES OF *PEPRILUS*. $\bar{x}$ = mean size (SL); $\bar{y}$ = mean of body proportion; N = number of specimens; a = y intercept; b = slope; CL-b = 95% confidence limits for b; r = correlation coefficient.

BODY PROPORTION	$\bar{x}$	$\bar{y}$	N	a	b	CL-b	r
Body Depth							
medius	121.6	63.1	100	–8.4	0.59	0.49–0.69	0.96
ovatus	85.6	52.1	90	4.6	0.56	0.50–0.62	0.99
simillimus	123.8	57.3	100	–4.6	0.50	0.43–0.57	0.97
snyderi	170.0	70.8	24	5.4	0.38	0.30–0.46	0.99
burti	82.0	44.9	90	1.7	0.53	0.46–0.60	0.99
triacanthus	108.4	48.3	100	3.1	0.42	0.35–0.49	0.98
paru	91.6	63.5	100	9.7	0.58	0.48–0.68	0.95
Eye Diameter							
medius	121.6	9.9	100	3.5	0.052	0.042–0.062	0.93
ovatus	85.6	7.9	90	1.5	0.074	0.067–0.081	0.97
simillimus	123.8	8.6	100	3.9	0.038	0.027–0.049	0.81
snyderi	170.0	11.2	24	3.3	0.046	0.037–0.055	0.97
burti	82.0	7.8	90	1.0	0.083	0.073–0.093	0.90
triacanthus	108.4	8.4	100	2.4	0.056	0.046–0.066	0.84
paru	91.6	9.0	100	1.8	0.078	0.070–0.086	0.90
Length of Upper Jaw							
medius	121.6	10.0	100	2.60	0.061	0.054–0.068	0.96
ovatus	85.6	6.8	90	0.59	0.072	0.065–0.079	0.98
simillimus	123.8	9.3	100	1.00	0.067	0.060–0.074	0.96
snyderi	170.0	13.2	24	2.20	0.065	0.060–0.070	0.99
burti	82.0	7.1	90	0.43	0.081	0.077–0.085	0.99
triacanthus	108.4	8.9	100	0.81	0.075	0.069–0.081	0.98
paru	91.6	7.5	100	1.30	0.068	0.062–0.074	0.97
Length of Pectoral Fin							
medius	122.2	47.0	100	–6.10	0.43	0.39–0.47	0.97
ovatus	85.8	32.4	90	–6.60	0.45	0.40–0.50	0.97
simillimus	123.8	41.6	100	1.70	0.32	0.25–0.39	0.93
snyderi	170.0	57.4	24	–0.57	0.33	0.27–0.39	0.99
burti	81.5	28.4	90	–3.00	0.38	0.32–0.44	0.98
triacanthus	108.3	34.9	100	–1.20	0.33	0.26–0.40	0.97
paru	92.1	35.9	100	–2.50	0.42	0.38–0.46	0.99
Depth of Caudal Peduncle							
medius	121.6	9.4	100	–3.30	0.104	0.088–0.120	0.95
ovatus	85.6	6.9	90	–0.67	0.090	0.077–0.103	0.97
simillimus	123.8	8.1	100	–1.10	0.075	0.062–0.088	0.95
snyderi	170.0	12.4	24	–2.10	0.085	0.079–0.091	0.99
burti	82.0	6.3	90	–0.37	0.081	0.074–0.088	0.99
triacanthus	108.4	7.6	100	–0.31	0.073	0.064–0.082	0.97
paru	91.6	8.4	100	–1.04	0.103	0.095–0.111	0.97

Sinaloa, Mex., S of Bahía Topolobampo, off I. San Ignacio and I. Macapule, 7–13 m, 10–14 February 1958); UCLA W58–218 (1:126.2, Gulf of Panama, 10 miles WNW I. Pacheca, 08°44′N, 79°13′W, 48 m, 8 March 1957); *UCLA W58–303 (14:124.3–156.0, Panama Bay, Punta Bay, Punta Chame and Punta Anton, 6–27 m, 6–9 September 1958); *UCLA W58–304 (8: 100.4–131.6, Panama Bay, between Punta de Hicacal and Rio Pasiga, 3–4 m, 7–9 September 1958); UCLA W58–305 (1:

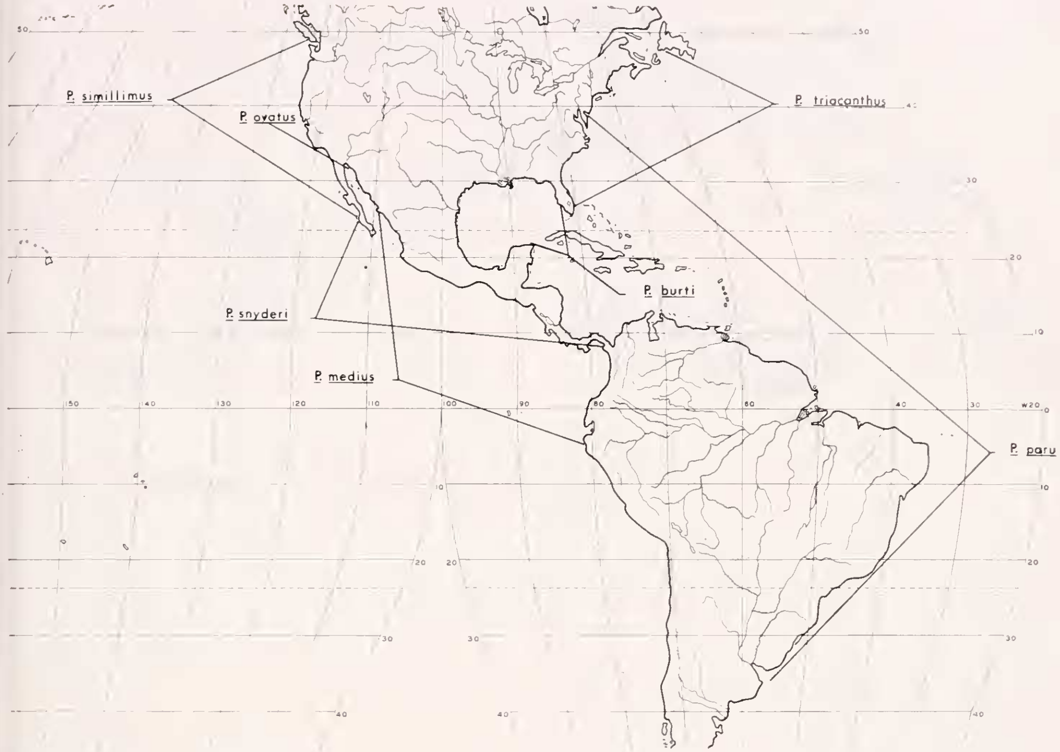


Figure 7. Distribution of the species of *Peprilus*.

136.0, Panama Bay between Rio Chico and Punta de la Plata, 3–6 m, 7–11 September 1958).

Diagnosis. P. medius is moderately elongate and is the only Pacific Coast species in the genus with moderately to extremely falcate dorsal and anal fins. Specifically and aside from the length of the lobes of the dorsal and anal fins, it is distinguished from the similar *P. ovatus* by having usually 21 rather than 19 caudal vertebrae; a more elongate body – mean body depth of 529 compared to 619 for *P. ovatus*, each in thousandths of SL; a mean number of dorsal fin-rays of 46.7 compared to 42.8 for *P. ovatus;* and usually three dorsal spines rather than frequently four as in *P. ovatus.* It is distinguished from *P. snyderi* by having a deeper body – mean body depth of 529 compared to 427 for *P. snyderi*, each in thousandths of SL; an eye diameter greater than the length of the snout; and 33 to 35 rather than 36 total vertebrae; and from *P. simillimus* by having a deeper body – mean body depth of 529 compared to 461 for *P. simillimus*, each in thousandths of SL; a mean number of anal fin-rays of 43.9 compared to 39.5 for *P. simillimus;* and 33 to 35 rather than 30 or 31 total vertebrae. The species differs from the related *P. paru* in the Atlantic by having a more elongate body – mean body depth of 529 compared to 710 for *P. paru*, each in thousandths of SL; a mean number of dorsal fin-rays of 46.9 compared to 42.9 for *P. paru;* and 33 to 35 rather than 29 to 31 total vertebrae.

Description. Proportional measurements are given in Table 7 and meristic values in Table 8. Body moderately elongate, moderately deep to deep, compressed; anterior dorsal profile moderately convex.

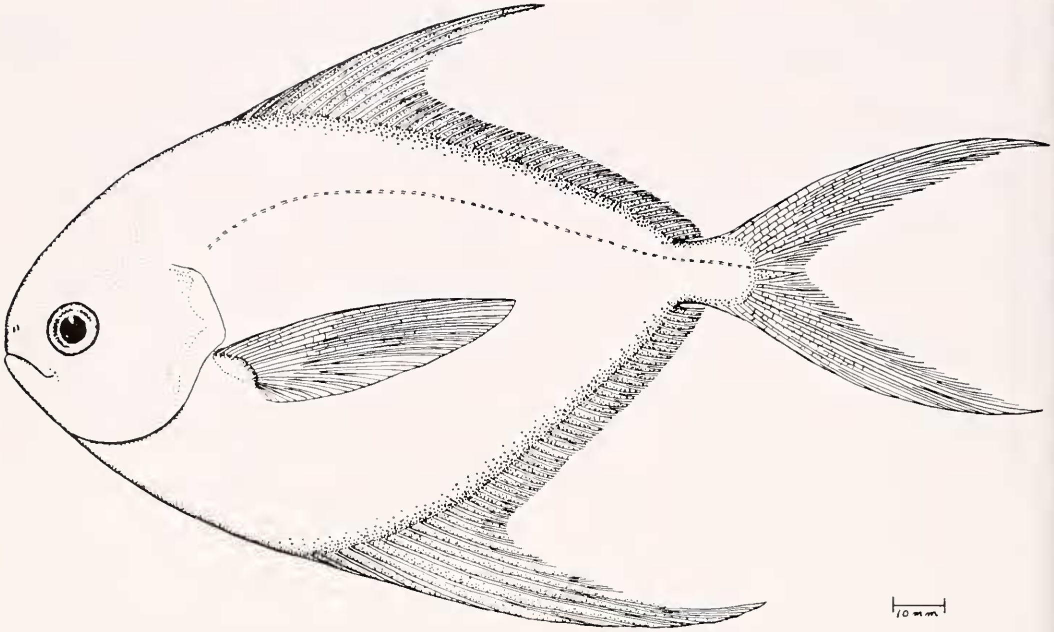


Figure 8 *Peprilus medius,* 141.3 mm SL, Golfo de Fonseco, Honduros, SIO H51-324.

Eye diameter greater than length of snout. Dorsal and anal fins moderately to extremely falcate, longest rays of anal six or more times the length of shortest anal ray; dorsal often slightly less falcate; both usually becoming more falcate with age. Dorsal and anal with three or four (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 22 to 40 per cent of total length. Subdermal canal system indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. Premaxillary teeth slightly recurved, pointed, simple. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 250 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from four to about 11 (Table 7) and from 1.2 to about 3.6 for meristic characters (Table 8). According to Simpson *et al.* (1960), V is a good measure of relative dispersion and usually a suitable measure of variability; it is useful in comparing the variability of samples or species.

The sample size of *P. medius* (Table 7) used is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all the species of *Peprilus,* is relatively constant (Table 5).

Geographic variation. No decided geographic variation was detected in *P. medius.* A slight tendency, however, for the median fins to be longer in the lower latitudes of the distribution was noted, but was too small to quantify.

Ontogenetic change. Few and moderate changes accompany growth in *P. medius* in a size range of about 50 to 189 mm SL.

TABLE 7. PROPORTIONAL MEASUREMENTS OF *PEPRILUS MEDIUS*. N = number of specimens; R = range of values; x̄ = mean; SE = standard error of mean; V = coefficient of variation. Size range, 50.0–189.0 mm SL; mean size, 124.4 mm SL.

	N	R	x̄	SE	V
In thousands of SL:					
Head length	162	260–384	295	1.61	6.96
Snout length	162	046–080	060	0.37	7.95
Eye diameter	162	061–113	082	0.64	9.87
Length of upper jaw	162	069–111	082	0.62	9.59
Interorbital width	162	077–109	091	0.41	5.78
Length of pectoral fin	160	290–442	386	2.13	6.99
Predorsal distance I	162	351–436	390	1.27	4.14
Predorsal distance II	162	239–312	273	1.18	5.52
Preanal distance	162	369–496	434	1.50	4.39
Maximum depth of body	182	459–618	529	2.34	5.98
Least depth of caudal peduncle	162	058–094	078	0.68	11.04
In thousandths of HL:					
Snout length	162	152–284	203	1.32	8.31
Eye diameter	162	235–333	279	1.29	5.86
Length of upper jaw	162	225–333	278	1.10	5.01
Interorbital width	162	240–352	307	1.49	6.18

With growth, head length and eye diameter decreases in size relative to SL (Fig. 9). The correlation coefficient in the size-on-size regression of eye diameter is, however, relatively high (Fig. 3; Table 6). Body depth, length of the pectoral fin, and depth of the caudal peduncle increase in size relative to SL with growth up to about 125 to 150 mm SL, beyond which the values become nearly constant (Figs. 9 and 12). The anterior lobes of the dorsal and anal fins tend to increase in length with growth (compare Figs. 8 and 18a).

TABLE 8. MERISTIC VALUES OF *PEPRILUS MEDIUS*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	158	42–51	46.7	0.12	3.19
Anal fin-rays*	157	40–47	43.9	0.11	3.03
Pectoral fin-rays	158	20–24	22.6	0.07	3.63
Total gill rakers	154	23–27	24.7	0.07	3.56
Total vertebrae	181	33–35	34.0	0.03	1.21
Lateral-line scales	23	105–117	–	–	–

* Excluding spines.

Distribution (Fig. 7). *P. medius* is known from off the Pacific Coast of northern South America, Central America, and Mexico northward to the southern region of the Gulf of California. The southern extent of the range is near Paita, Peru, about 5°S, and just south of Golfo de Guayaquil. The northern known limit of the range is near Bahía Topolobampo, Sinaloa, Mexico, about 25°30′N. One specimen is known from the Galapagos Islands, but was not examined in this study (128 mm SL, TABL uncat.).

Taxonomic comments. The holotype of *Stromateus medius* Peters is very similar to specimens identified as *Peprilus* or *Palometa palometa*. The supposed anal ray count of 32 for the holotype of *S. medius* is incorrect; the correct value is 42, within the range of values for *P. palometa*. The count can be made accurately only by examining the radiograph of the holotype since the anterior portion of the anal fin is externally mutilated. I have thus placed the two names, *S. medius* and *P. palometa*, in synonymy of *Peprilus medius*.

It has been a common practice to identify questionable stromateids from the Gulf of California with either *Palometa media* or *Peprilus medius*. A distinct population does exist in the northern Gulf of California and is described below as new.

Peprilus ovatus sp. n.

Figures 10, 18b

Holotype. A 128.7 mm SL specimen, USNM 203304; 3–5 February 1949, Gulf of California, Sonora, Mexico, about 20 miles SW of Golfo de Santa Clara near the mouth of the Colorado River, shrimp trawl, 13 to 27 m depth.

Paratypes. Two, 56.6, 118.4 mm SL, LACM 30175–1 and –2; data as above for holotype.

Two, 56.9, 123.9 mm SL, MCZ 46202; data as above for holotype.

Thirty-six, 38.3–126.0 mm SL, UCLA W49–55; data as above for holotype.

Additional material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). All specimens are from the northern Gulf of California. *CAS 24158 (15:41.4–127.5 mm, Sonora, Mexico, 10 miles off Santa Clara, 5 February 1952, 2 CS); *SIO H47–53 (2:62.5, 67.7, Baja California, between San Felipe and mouth of Colorado River, 31°18′–22′N, 114°47′–50′W, 4–9 m, 6–9 April 1947, shrimp trawler FELIPE ANGELES); *SIO 58–164 (3:51.5–75.6, Baja Calif., 10 miles N of San Felipe, 4 April 1956); *SIO 63–484 (6:55.9–84.3, mouth of Colorado R.); *UCLA W49–91 (36:37.5–124.8, Baja Calif., about 10 miles SE of San Felipe, February, 1950); *UCLA W49–422 (4:70.6–78.0, Baja Calif., between San Felipe and mouth of Colo. R., 6–9 April 1947); *UCLA W49–423 (2:80.8, 84.1, Baja Calif., San Felipe Bay, 10 April 1947); UCLA W49–429 (1:83.5, Baja Calif., off Punta Diggs S of San Felipe, 10 April 1947); *UCLA W53–196 (29:63.2–88.0, Baja Calif., between San Felipe and mouth of Colo. R., 6–9 April 1947, same collection as UCLA W49–422); *UCLA W53–198 (3:69.0–87.9, Baja Calif., San Felipe Bay, 10 April 1947); *UCLA W54–366 (1:145.2, Baja Calif., 2 to 3 miles N of Punta Diggs, about 7 miles S of San Felipe, 11 m, 23 September 1954, shrimp trawler SAN LUIS); *UCLA 55–2 (9:45.4–132.5, Baja Calif., Punta Diggs, 9 miles E of San Felipe, 24 m, 1–2 February 1955, shrimpboat YUKY); UCLA W55–23 (2: 60.3, 111.6, Baja Calif., 1 mile S of San Felipe, 0–7 m, 9–11 March 1955, 600 ft

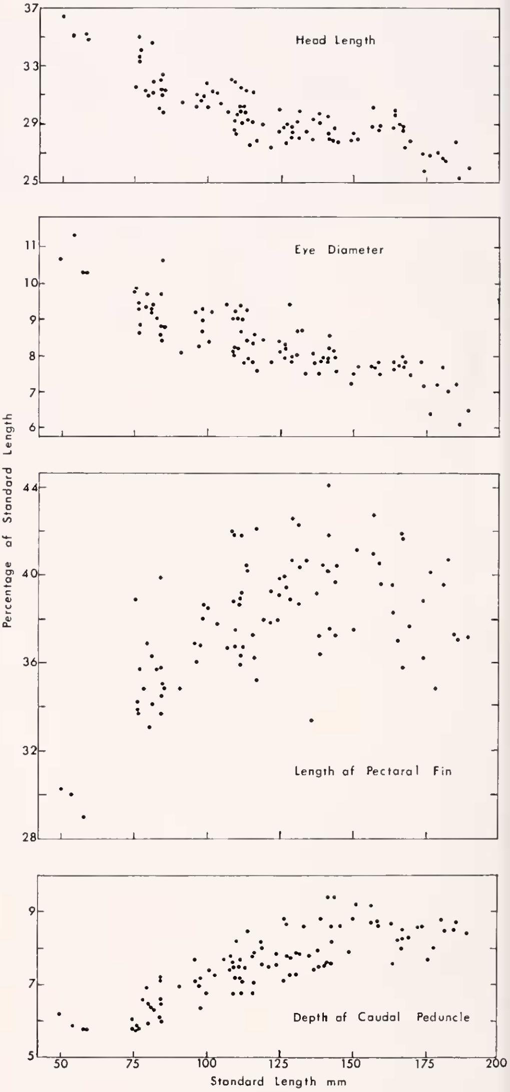


Figure 9. Ratio-on-size scatter diagrams for four morphometric characters of *Peprilus medius.*

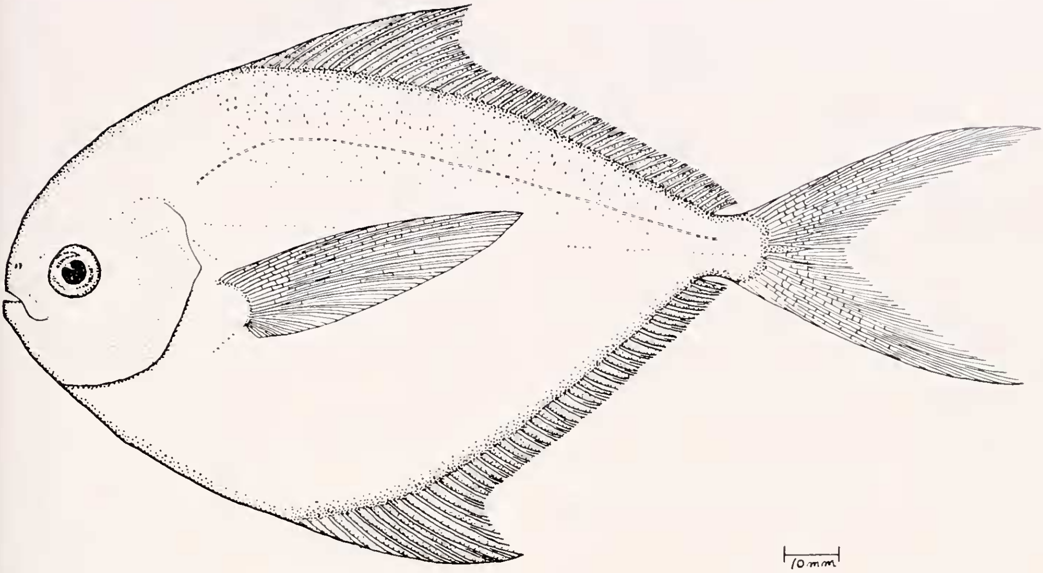


Figure 10. *Peprilus ovatus*, holotype, 128.7 mm SL, 20 miles SW of Golfo de Santa Clara, northern Gulf of California, USNM 203304.

beach seine); *UCLA W55–27 (6:56.2–110.6, Baja Calif., Punta Diggs, 5–10 miles S of San Felipe, 26 m, 11 March 1955, shrimpboat YUKY); *UCLA W55–28 (3: 112.7–132.0, Baja Calif., 4 to 5 miles N of San Felipe, 27 m, 11 March 1955, shrimpboat YUKY).

Diagnosis. *P. ovatus* is a short, deep-bodied species with slightly falcate dorsal and anal fins. It is distinguished from *P. snyderi* by having a much deeper body – mean body depth of 619 compared to 427 for *P. snyderi*, each in thousandths of SL; an eye diameter greater than the length of the snout; a mean number of dorsal fin-rays of 42.8 compared to 46.5 for *P. snyderi;* and 31 to 33 rather than 36 total vertebrae. It is distinguished from *P. simillimus* by having a much deeper body – mean body depth of 619 compared to 461 for *P. simillimus;* an eye diameter greater than the length of the snout; a mean number of anal fin-rays of 43.0 compared to 39.5 for *P. simillimus;* and 31 to 33 rather than 30 or 31 total vertebrae. Characters that distinguish *P. ovatus* from *P. medius* are listed in the diagnosis of the latter species. The specific epithet, *ovatus,* is from the Latin and is descriptive of the short, deep body of the species.

Description. Proportional measurements are given in Table 9 and meristic values in Table 10. Body ovate, deep, compressed; anterior dorsal profile moderately convex. Eye diameter greater than length of snout. Dorsal and anal fins slightly falcate, the longest dorsal ray three to six times the length of the shortest dorsal ray, the longest anal ray two to five times the length of the shortest anal ray. Dorsal fin with three or four (usually four) small, bladelike spines preceding the rays; anal fin with three or four (usually three) spines preceding the rays. Dorsal and anal fins originating at about the same level anteriorly, and the bases about equal in length. Caudal fin long to very long, deeply forked, about 24 to 35 per cent of total length. Lateral line of trunk highly arched

TABLE 9. PROPORTIONAL MEASUREMENTS OF *PEPRILUS OVATUS*. Symbols as in Table 7. Size range, 37.5–145.2 mm SL; mean size, 79.0 mm SL.

	N	R	$\bar{x}$	SE	V
In thousandths of SL:					
Head length	158	259–325	296	1.08	4.60
Snout length	158	052–074	063	0.39	7.75
Eye diameter	158	078–115	093	0.62	8.35
Length of upper jaw	158	065–094	080	0.43	6.75
Interorbital width	158	080–106	092	0.41	5.62
Length of pectoral fin	154	267–441	360	2.68	9.26
Predorsal distance I	158	369–465	408	1.52	4.67
Predorsal distance II	158	259–347	298	1.33	5.62
Preanal distance	158	427–552	481	2.13	5.57
Maximum depth of body	163	542–676	619	2.36	4.86
Least depth of caudal peduncle	158	060–094	079	0.54	8.59
In thousandths of HL:					
Snout length	158	176–244	213	1.23	7.23
Eye diameter	158	267–377	315	1.69	6.76
Length of upper jaw	158	234–313	271	1.20	5.55
Interorbital width	158	263–357	311	1.72	6.97

TABLE 10. MERISTIC VALUES OF *PEPRILUS OVATUS*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	145	40–46	42.8	0.12	3.27
Anal fin-rays*	147	40–46	43.0	0.12	3.40
Pectoral fin-rays	150	19–23	21.4	0.06	3.50
Total gill rakers	146	21–26	23.6	0.07	3.35
Total vertebrae	157	31–33	32.0	0.02	0.81
Lateral-line scales	–	–	–	–	–

* Excluding spines.

anteriorly, following dorsal profile posteriorly. Subdermal canal system visible as indistinct lines on the body; dendritic canals on top of head and nape often ill-defined. A series of medium-sized, irregularly-spaced, slitlike pores frequently visible along dorsal and upper ventral surfaces. Premaxillary teeth slightly recurved, pointed, and simple. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 200 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from about 4.6 to 9.3 (Table 9) and from 0.8 to 3.5 for meristic characters (Table 10). These values indicate that the relative dispersion of character values is nearly as great as that of its presumed closest relative, *P. medius*. It might be expected that such a species of restricted distribution would be less variable than that of the wide-ranging species from which it is derived.

The sample size is considered to be reasonably adequate. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all the species of *Peprilus*, is relatively constant (Table 5).

Geographic variation. No geographic variation was found in *P. ovatus* because of its apparently restricted distribution.

Ontogenetic change. Few and moderate changes accompany growth in *P. ovatus* in a size range of about 40 to 145 mm SL. With growth, eye diameter and head length decrease in size relative to SL, while the length of the pectoral fin and the depth of the caudal peduncle increase in size relative to SL (Fig. 11). The length of the pectoral fin, however, becomes nearly constant beyond about 100 mm SL. In contrast to the situation in the related *P. medius*, body depth in *P. ovatus* decreases in size relative to SL with growth (Fig. 12). The anterior lobes of the dorsal and

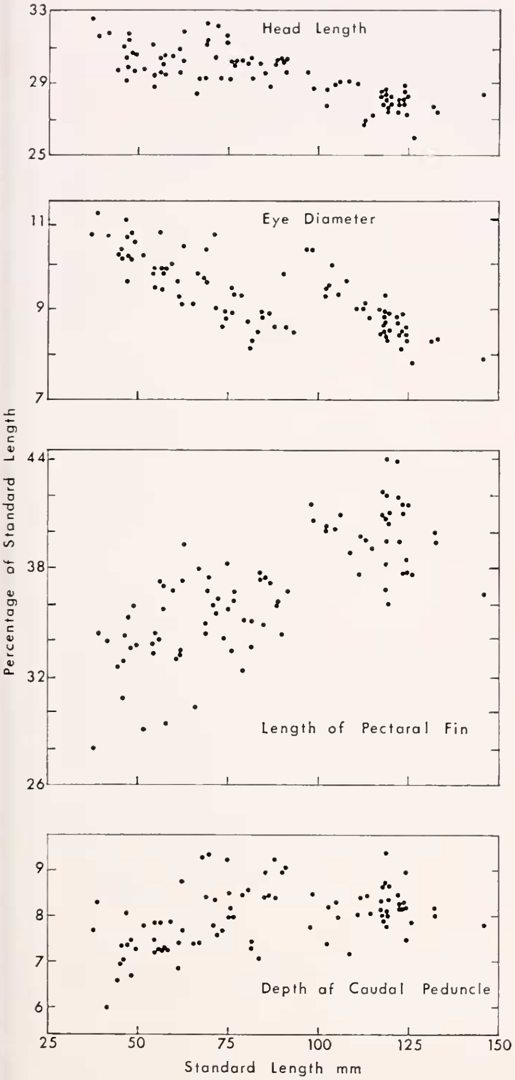


Figure 11. Ratio-on-size scatter diagrams for four morphometric characters of *Peprilus ovatus*.

anal fins tend to slightly increase in length with growth (compare Figs. 10 and 18b).

Distribution (Fig. 7). *P. ovatus* is known only from the northern Gulf of California from Punta Diggs south of San Felipe, Baja California, northward to the mouth of the Colorado River and from Golfo de Santa Clara, Sonora, to the mouth of the Colorado River.

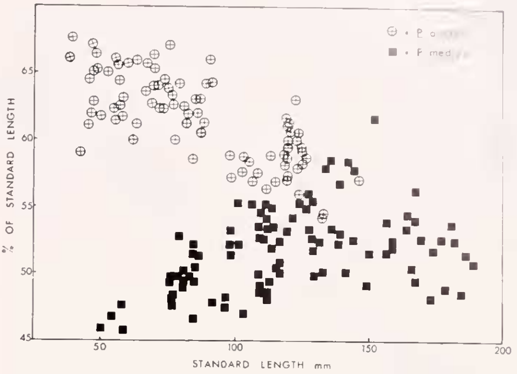


Figure 12. Ratio-on-size scatter diagram of body depth for *Peprilus medius* and *Peprilus ovatus*.

Taxonomic comments. See taxonomic comments under *P. medius.*

Peprilus simillimus (Ayres, 1860)
Figures 13, 18c

Poronotus simillimus Ayres, 1860: 84, fig. 1 (original description, San Francisco, California, holotype, a CAS specimen apparently destroyed by fire in 1906).

Stromateus simillimus, Jordan and Gilbert, 1881: 46; Jordan and Gilbert, 1882a: 451; Fordice, 1884: 314.

Rhombus (*Palometa*) *simillimus,* Jordan and Evermann, 1896: 967, *Palometa* erected as a subgenus.

Palometa simillima, Jordan and Evermann, 1898: 2849, subgenus *Palometa* elevated to generic level; Jordan, Evermann, and Clark, 1930: 266; Roedel, 1953: 81, fig. 78; Batts, 1960: 146, occurrence in Washington; Berry and Perkins, 1966: 673, distribution in California Current area; High, 1966: 53, fig. 1, occurrence in Puget Sound.

Peprilus simillimus, Clemens and Wilby, 1946: 201, fig. 38; J. L. Hart, 1949: 101; Haedrich, 1967: 107.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BC 62–242 (6:151.5–169.5 mm, British Columbia, Strait of Georgia, Pender Harbor and

Bargain Harbor, 4 radiographed); *BC 63–1447 (1:143.0, British Columbia, San Juan de Fuca Strait); CAS 1546 (1:168.5, San Francisco, Calif.); *CAS 1552 (1:157.0, San Francisco, Calif.); CAS 21929 (1:92.3, San Francisco Bay, Calif., 4 May 1955); *CAS 21943 (1:105.9, San Francisco Bay, Calif., 22 May 1955); *LACM 401 (11 meas.: 98.2–131.8, Calif., Los Angeles County, Long Beach, Belmont Shores, 25 October 1957, 58 radiographed); *LACM 3000 (1:76.2, Calif., Los Angeles Co., Long Beach, Belmont Shores, 19 October 1962); *LACM 21044 (1:68.2, Calif., Los Angeles Co., Venice Pier, 15 August 1914); MCZ 16885 (2:118.0, 121.5, San Francisco, Calif.); MCZ 17337 (1:192.5, San Francisco, Calif.); MCZ 23394 (1:202.0, San Francisco, Calif.); MCZ 23395 (1:168.0, San Francisco, Calif.); MCZ 23399 (1: 174.0, San Francisco, Calif.); *SIO H52–221 (4:28.4–49.8, Pacific Ocean, Baja Calif., San Martin I., Hassler Cove, found in bell of jellyfish, *Pelagia* sp., 14 September 1952, 1 radiographed, 1 CS); *SIO 59–70 (1:71.0, Pacific Ocean, Baja Calif., 26°48′N, 113°25′W, 3 July 1958); *SIO 60–394 (1:86.4, Pacific Ocean, Baja Calif., Sebastián Vizcaíno Bay, 28°34.5′N, 114°24′W, 19 August 1960); *SIO 60–409 (1:48.0, Calif., San Diego Co., La Jolla Bay, found in bell of jellyfish, *Pelagia* sp., 6 July 1960); *SIO 62–236 (1:137.5, Gulf of Calif., Baja Calif., Bahía de Los Angeles, 28°55′–56′N, 113°31′–33′W, 20 m, 26 April 1962); *SIO 62–580 (1:68.7, Calif., Imperial Co., on beach at Salton Sea, apparently a live-bait transfer, 3 September 1962); *SIO 62–681 (20 meas.:78.7–144.9, Calif., off San Diego, 32°46.5′N, 117°18.5′–19.7′W 0–82 m, 1 September 1962, R/V JOHN N. COBB, Cobb Mark II pelagic trawl, 23 radiographed); *SIO 64–641 (5:107.4–129.0, Pacific Ocean, Baja Calif., E of Cedros I., 2 miles from shore, 15 m, 17 August 1961); *SIO 64–747 (2:78.2, 86.0, Pacific Ocean, Baja Calif., Bahía Magdalena, from bait sample, 7 September 1954, M/V MARY C. CANAS); *SU 4382 (6:96.3–158.5, Monterey Bay, Calif.); SU 48000 (1:85.0, off Oceanside, Calif., 17 November 1943); *USNM 4472 (1:172.0, San Francisco, Calif.); *USNM 26800 (4:101.0–143.0, San Diego, Calif.); *USNM 26910 (4:113.0–144.0, Santa Barbara, Calif.); *USNM 38015 (1:108.0, San Diego, Calif.); *USNM 42045 (2:135.4, 150.0, Wash., Seattle market); *USNM 52998 (1:168.0, Calif., San Pedro market); *UCLA W56–360 (4: 79.0–96.4, Pacific Ocean, Baja Calif., Turtle Bay, 27°41′N, 114°53′W, 0–7 m, 22 July 1956, bait net); *UW 13405 (4:140.3–153.3, Wash., Strait of Georgia, Bellingham Bay, 8 February 1946); *UW 14656 (9:164.7–198.0, Wash., Puget Sound, Fletcher Bay, 11 December 1959); *UW 18210 (6:119.3–152.4, Wash., Orcas I., East Sound, 0–27 m, 10 September 1963).

Diagnosis. P. simillimus is an elongate, shallow to moderately deep species with only slightly falcate dorsal and anal fins. The species is distinguished from *P. snyderi* by having a mean number of dorsal fin-rays of 44.8 compared to 46.5 for *P. snyderi;* a mean number of anal fin-rays of 39.5 compared to 42.0 for *P. snyderi;* and 30 or 31 rather than 36 total vertebrae. Characters that distinguish *P. simillimus* from *P. medius* and *P. ovatus* are listed in the diagnosis of each of these species, respectively. *P. simillimus* is distinguished from the similar *P. triacanthus* by having no row of relatively large pores beneath the anterior half of the dorsal fin. The specific epithet, *simillimus,* is from the Latin, "similis," meaning like or resembling; the species was so named because of its similarity to *P. triacanthus.*

Description. Proportional measurements are given in Table 11 and meristic values in Table 12. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly convex. Eye diameter about equal to the length of the snout; eye relatively small. Dorsal and anal fins slightly falcate, the longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the

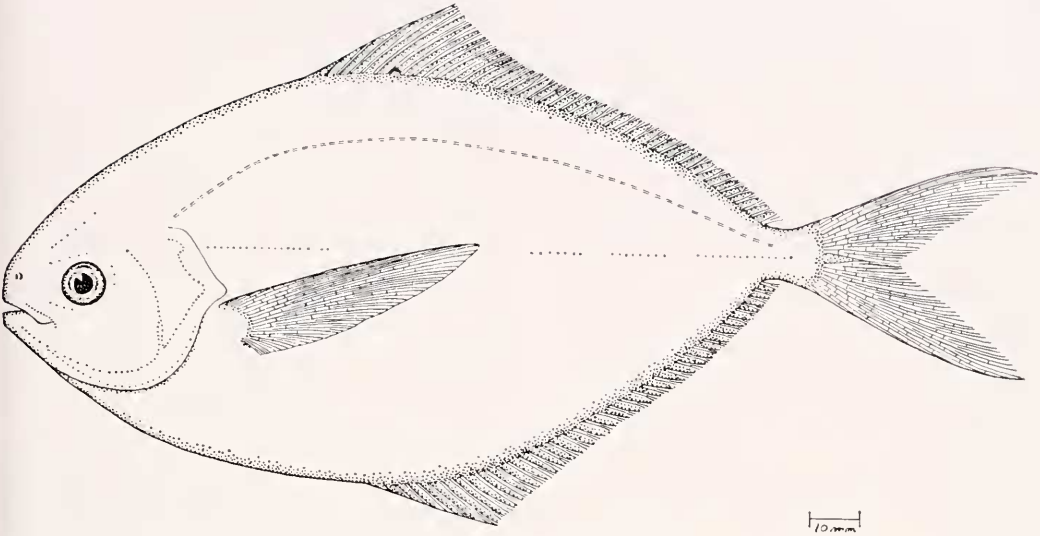


Figure 13. *Peprilus simillimus*, 164.7 mm SL, Puget Sound, Washington, UW 14656.

length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) spines anterior to the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long, moderately to deeply forked, about 18 to 32 per cent of total length. Subdermal canal system visible as indistinct parallel lines on body in preserved material; dendritic canals on top of head and nape distinct. Premaxillary teeth slightly recurved, mostly pointed, simple, but a few on a particular specimen may have two or three small cusps. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Except for eye diameter, coefficients of variation (V) for proportional measurements range from 3.8 to about 9 (Table 11) and from 1.2 to 4.2 for meristic characters (Table 12). The V value for eye diameter as a percentage of SL is 17.44, a high value resulting from allometric growth.

The sample size (Table 11) of *P. simillimus* used is considered to be reasonably adequate, and specimens from almost all parts of the known range have been examined. Except for vertebral number, ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). Vertebral number, as in all species of *Peprilus,* is relatively constant (Table 5).

Geographic variation. There is slight but inconclusive evidence that northern members of *P. simillimus* are larger and deeper-bodied. The dorsal, anal, and caudal fins of northern specimens seem to be shorter and less conspicuous. The differences are slight in the dorsal and anal fins, but more prominent in the caudal fin. Length of the caudal fin expressed as a percentage of the total length in specimens from San Francisco to British Columbia is less on the average than in specimens taken from Monterey to Baja California (Fig. 14). Although the ranges of the two groups overlap, the difference in the means is highly significant with a probability of much less than 0.001 using a two-tailed Student's *t*-test.

The functional significance of shorter or lower fin lobes in northern populations of fish species is apparently unknown. Per-

TABLE 11. PROPORTIONAL MEASUREMENTS OF *PEPRILUS SIMILLIMUS*. Symbols as in Table 7. Size range, 28.4–202.0 mm SL; mean size, 123.8 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	109	252–408	285	2.28	8.35
Snout length	109	058–081	070	0.45	6.74
Eye diameter	109	050–119	073	1.22	17.44
Length of upper jaw	109	064–100	076	0.64	8.82
Interorbital width	109	076–110	089	0.53	6.26
Length of pectoral fin	109	272–379	336	2.28	7.41
Predorsal distance I	103	338–407	369	1.37	3.76
Predorsal distance II	109	222–339	263	1.82	7.23
Preanal distance	109	402–518	440	2.01	4.78
Maximum depth of body	109	394–517	461	2.01	4.57
Least depth of caudal peduncle	109	055–074	065	0.43	6.83
In thousandths of HL:					
Snout length	109	192–287	246	2.11	8.95
Eye diameter	109	188–347	255	2.62	10.71
Length of upper jaw	109	218–323	267	1.63	6.39
Interorbital width	109	259–369	314	2.07	6.89

TABLE 12. MERISTIC VALUES OF *PEPRILUS SIMILLIMUS*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	98	41–48	44.8	0.16	3.50
Anal fin-rays*	100	35–44	39.5	0.15	3.67
Pectoral fin-rays	107	19–23	21.1	0.06	3.13
Total gill rakers	75	23–26	23.9	0.12	4.18
Total vertebrae	160	30–31	30.2	0.03	1.19
Lateral-line scales	9	95–110	–	–	–

* Excluding spines.

haps the difference is allied to differential growth rates as influenced by regional conditions of temperature. The shorter fin lobes may possibly be associated with surface-volume ratios and with adaptations to cooler temperatures.

Ontogenetic change. Few and moderate changes accompany growth in *P. simillimus* in a size range of about 28 to 202 mm SL. With growth, head length and eye diameter decrease in size relative to SL while depth of body and of caudal peduncle remain nearly constant (Fig. 15). The correlation coefficient of the size-on-size regression of eye diameter is the lowest among members of the genus (Fig. 3; Table 6). The length of the pectoral fin increases slightly in size relative to SL with growth up to about 125 mm SL, beyond which there is a slight decrease (Fig. 15).

Distribution (Fig. 7). *P. simillimus* is known along the Pacific Coast of North America from southern Baja California to southern British Columbia. The southern limit of the range is in the vicinity of Bahía Magdalena, Baja California, at about 24°30′N. One specimen here referred to as *P. simillimus* is known from the Gulf of California: a female, 137.5 mm SL, from Bahía de Los Angeles, Baja California, 28°55′–56′N, 113°31′–33′W (SIO 62–236). The northern known extents of the range are near Clayoquot Sound on the west Coast of Vancouver Island, near Nanaimo on the east coast of the Island, and near the mouth of the Fraser River at Vancouver, British Columbia, all at about 49°N.

Taxonomic comments. Ayres (1860) in his original description of this species placed it "with doubt" in the genus *Poronotus*, noting that it lacked the relatively large dorsal pores characterizing *Poronotus triacanthus*. Until he received Gill's (1861) "Catalogue of the fishes of the eastern coast of North America from Greenland to Georgia," Ayres had recorded the new

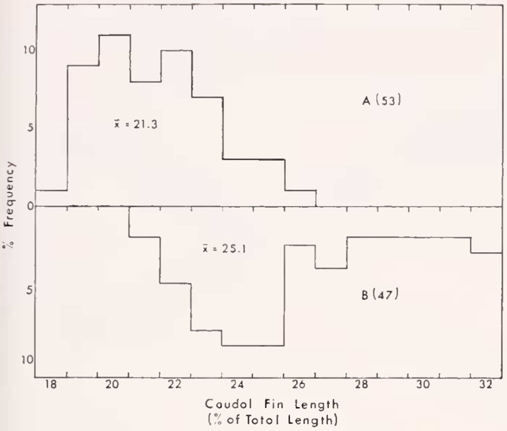


Figure 14. Geographic variation of caudal fin length in *Peprilus simillimus*: A = specimens collected between British Columbia and San Francisco; B = specimens collected between Monterey, California, and southern Baja California; numbers in parentheses are the sample sizes; x̄ = mean. The means are highly significantly different at the 2 per cent level (two-tailed Student's *t*-test).

species in his manuscript notes as *Peprilus simillimus.* Since Gill reserved the genus *Peprilus* for the deep-bodied species with falcate median fins, and the genus *Poronotus* for the elongate species with relatively large dorsal pores, Ayres with reluctance placed the new species in the genus *Poronotus* because of the overall similarity to *Poronotus triacanthus.*

This species is often referred to in faunal and fishery works as *Palometa simillima,* after Jordan and Evermann's (1898) designation.

The common names of *P. simillimus* on the Pacific Coast, "California pompano," "Pacific pompano," or "pompano," are somewhat misleading since "pompano" is most frequently used in reference to certain fishes of the family Carangidae. A more appropriate name might be "Pacific butterfish" after the familiar butterfish, *P. triacanthus,* of the Atlantic Coast.

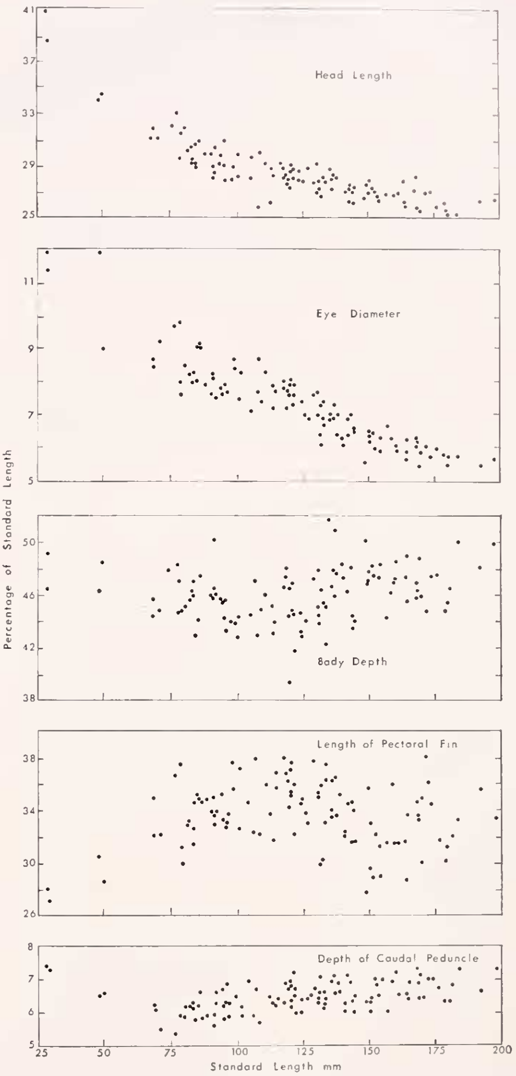


Figure 15. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus simillimus.*

Peprilus snyderi Gilbert and Starks, 1904
Figures 16, 18d

Peprilus snyderi Gilbert and Starks, 1904: 87, fig. 23, pl. XII (original description, Panama Bay, holotype not seen; three paratypes seen, 2:188.0, 193.0 mm SL. SU 7009; 1:182.3, USNM 50448); Meek and S. F. Hildebrand, 1925: 413; Haedrich, 1967: 107.

Palometa snyderi, Jordan, Evermann, and Clark, 1930: 267.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless other-

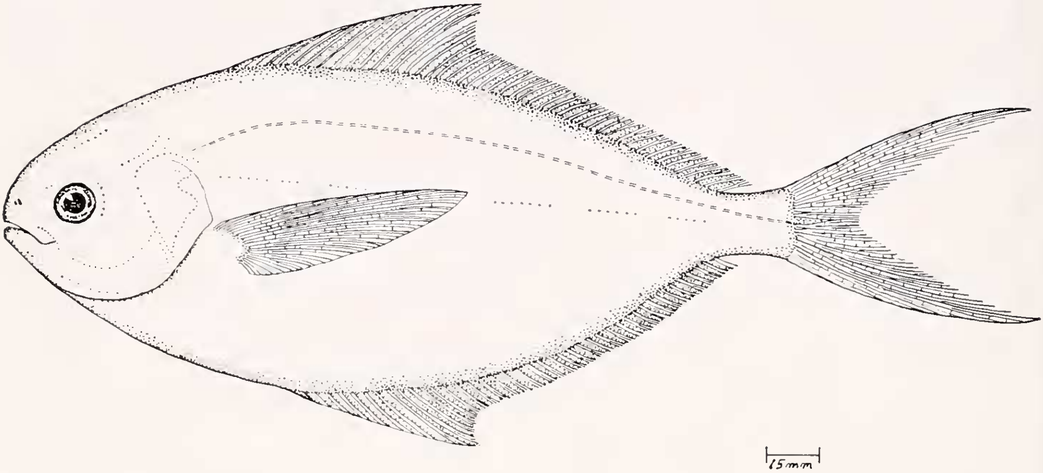


Figure 16. *Peprilus snyderi,* 227.0 mm SL, Acapulco market, Mexico, BC 61-126.

wise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). *BC 59–247 (1:205.0 mm, Mazatlán, Mexico); *BC 59–687 (3:190.0–213.0, Panama City market); *BC 60–25 (1:193.0, Mex., Golfo de Tehuantepec, Puerto Arista to Salina Cruz); *BC 61–126 (1:227.0, Mex., Acapulco market); *FMNH 73840 (1:227.0, Mex., 1–5 miles off Chiapas coast at Guatemala border to above San Benito, 18–27 m, 14–18 December 1954); IMS 1310 (1:143.6, Mex., Salina Cruz market, 16 August 1963); *LACM 8859–2 (3:152.5–159.2, Gulf of California, 24°29′N, 110°26′W, 0–15 m captured in 82–110 m water, 6 April 1964, R/V ALASKA); *SIO H50–181 (3:238.0–245.0, Pacific Ocean, Baja Calif., Bahía San Juanico, San Juanico Anchorage, 26°15′N, 112°28′W, 12 April 1950, snag hooks); *SU 7009 (2:188.0, 193.0, paratypes, Panama Bay); *USNM 50448 (1:182.3, paratype, Panama Bay); *UCLA W53–267 (1:232.0, Panama City market, 23 June 1953); *UCLA W55–23 (1:179.0, Gulf of Calif., Baja Calif., 1 mile S of San Felipe, 0–7 m, 9–11 March 1955, 600 ft beach seine); *UCLA W56–113 (1:121.2, Gulf of Calif., Sinaloa, Mex., just S of mouth of Bahía Topolobampo, 6–11 m, 24 May 1956); *UCLA W56–129 (4:42.1–65.7, Jalisco, Mex., Bahía de Banderas, 20°32′N, 105°17′W, 0–7 m, 18 March 1956, bait net, 1 CS).

Diagnosis. P. snyderi is an elongate, wide-ranging, rarely-collected species with slightly falcate dorsal and anal fins. Characters that distinguish *P. snyderi* from *P. medius, P. ovatus,* and *P. simillimus,* are listed in the diagnosis of each of these species, respectively.

Description. Proportional measurements are given in Table 13 and meristic values in Table 14. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly convex. Eye diameter about equal to the length of the snout; eye relatively small. Dorsal and anal fins slightly falcate, the longest dorsal ray three to five times the length of the shortest dorsal ray, the longest anal ray two to five times the length of the shortest anal ray. Dorsal and anal with two or three (usually three) small spines preceding the rays; spines appear to be somewhat smaller and less conspicuous than in other members of the genus. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long, moderately to deeply forked, about 20 to 30 per cent of total length. Scales

TABLE 13. PROPORTIONAL MEASUREMENTS OF *PEPRILUS SNYDERI*. Symbols as in Table 7. Size range, 42.1–245.0 mm SL; mean size, 170.0 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	24	262–380	297	6.97	11.50
Snout length	24	059–083	068	1.23	8.85
Eye diameter	24	057–103	070	2.83	19.80
Length of upper jaw	24	066–107	081	2.17	13.14
Interorbital width	24	079–104	087	1.14	6.43
Length of pectoral fin	22	289–361	329	3.34	4.78
Predorsal distance I	24	332–430	364	6.18	8.32
Predorsal distance II	24	224–315	253	5.79	11.22
Preanal distance	24	367–505	424	7.38	8.53
Maximum depth of body	24	371–503	427	7.35	8.43
Least depth of caudal peduncle	24	050–082	071	1.75	12.10
In thousandths of HL:					
Snout length	24	191–250	230	2.84	6.05
Eye diameter	24	209–279	234	4.40	9.21
Length of upper jaw	24	250–290	272	1.96	3.53
Interorbital width	24	217–322	295	5.19	8.62

apparently somewhat less deciduous than in other members of the genus. Subdermal canal system visible as indistinct parallel lines on body in preserved material; dendritic canals on top of head and nape distinct. Premaxillary teeth slightly recurved, mostly pointed, simple, but a few on a particular specimen may have two or three small cusps. Swimbladder not seen in this species. Coloration as described for the genus. Maximum length probably 300 mm SL.

Variation. Except for eye diameter, coefficients of variation (V) for proportional measurements range from 3.5 to 13.1 (Table 13). The V values for meristic characters range from 2.9 to 4.2, excluding vertebral number which showed no variation (Table 14). The V value for eye diameter as a percentage of SL is 19.8. This range of V values is wider than for other species and may be at least partially explained by the small sample size (24), which consisted of several large fish and a few small fish.

TABLE 14. MERISTIC VALUES OF *PEPRILUS SNYDERI*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	24	43–49	46.5	0.28	2.88
Anal fin-rays*	23	40–44	42.0	0.30	3.35
Pectoral fin-rays	22	21–23	22.3	0.15	3.14
Total gill rakers	18	23–26	24.1	0.24	4.23
Total vertebrae	23	36	36.0	0.00	0.00
Lateral-line scales	12	110–130	–	–	–

* Excluding spines.

Geographic variation. No geographic variation was noted in this species.

Ontogenetic change. Few and moderate changes accompany growth in *P. snyderi* although the sample, 24 specimens between 42 and 245 mm SL, was small and lacked individuals between 60 and 120 mm. With growth, head length, eye diameter, and body depth decrease in size relative to SL while the relative depth of the caudal peduncle increases slightly and the relative length of the pectoral fin remains nearly constant (Fig. 17).

Distribution (Fig. 7). *P. snyderi* is known along the Pacific Coast from Panama Bay northward to the upper part of the Gulf of California near San Felipe (about 31°N) and to Bahía San Juanico (about 26°15′N) on the outer coast of Baja California. Collections from intermediate localities are few, but the species probably occurs along this entire coastal region.

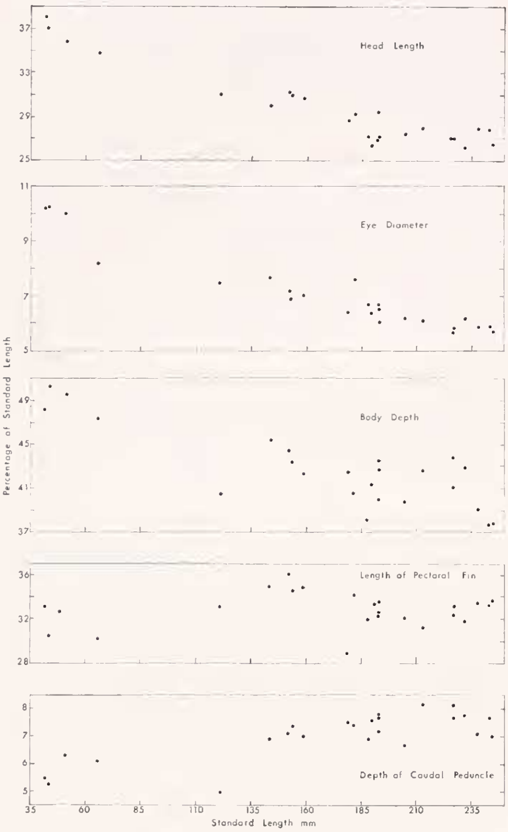


Figure 17. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus snyderi.*

Peprilus burti Fowler, 1944

Figures 19, 31

Poronotus triacanthus (not of Peck, 1804), Fowler, 1933: 61, Breton Island, Louisiana (misidentification); Briggs, 1958: 292, in part, Gulf of Mexico populations; Caldwell, 1961: 19, pl. 10, in part, bottom fish in photograph, Gulf of Mexico *Peprilus burti* synonymized with Atlantic *Poronotus triacanthus.*

Peprilus burti Fowler, 1944: 1, fig. 1 (original description, Breton Island, Louisiana, holotype seen, 113.3 mm SL, ANSP 55841; five paratypes seen, 2:73.3, 82.0, ANSP 55842–55843; 3:66.5–71.5, Galveston, Texas, ANSP 70943–70945); Haedrich, 1967: 108.

Poronotus burti, Collette, 1963: 582, valid species based on vertebral number.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). All localities are in the Gulf of Mexico. *ANSP 55841 (1:113.3 mm, holotype of *Peprilus burti* Fowler, 1944, Breton I., Louisiana, November, 1930); *ANSP 55842, 55843 (2:73.3, 82.0, paratypes of *Peprilus burti* Fowler, 1944, Breton I., La., November, 1930); *ANSP 70943 to 70945 (3:66.5–71.5, paratypes of *Peprilus burti* Fowler, 1944, Galveston, Texas, 1943); FSBC 372 (10:34.4–47.3, Florida, Escambia County, E of Pensacola Bay Bridge, 1 February 1958); FSBC 1640 (1:44.5, Fla., Pinellas Co., Madeira Beach, February, 1960); FSBC 2283 (6:96.2–106.1, Mississippi, Horn I., 27 October 1962); FSBC 3211 (1:63.6, Fla., Tampa Bay, grass flats, 9 October 1964); FSBC 3832 (1:71.2, Fla., Tampa Bay, 23 February 1966); FSBC 3954 (1:86.0, Fla., Pinellas Co., 27 December 1966, R/V CORTEZ); IMS 324 (1:80.5, Tex., Green Bayou, 11–15 m, 23 October 1950); IMS 327 (1:24.8, Port Aransas, Tex., from *Stomolophus* medusa, 27 November 1950; 1:28.2, Port Aransas, Tex., tide trap, 16 June 1950; 2:29.5, 30.0, Port Aransas, Tex., Humble Docks, dipnet, 1 May 1948); IMS 328 (5:79.0–88.8, 60–70 miles S of Port Aransas, Tex., 33–42 m, 13–16 May 1951); IMS 329 (1:120.8, 100 miles S of Port Isabel, Tex., 57–68 m, 6–11 March 1951; 2:82.5, 109.0, 40–60 miles S of Port Aransas, Tex., 22–33 m, 6–11 July 1951); IMS 330 (1:122.6, Mexico, Punta Frontera, 24–37 m, 29 July to 7 August 1951; 1:128.8, Tex., Corpus Christi Pass, 33–42 m, 22–23 January 1951); IMS 981 (3:100.8–107.9, Port Aransas, Tex., 37 m, 24 July 1962); IMS 1179 (3: 98.7–105.3, Port Aransas, Tex., 10 July 1962); IMS uncat. (8:28.4–88.4, Port Aransas, Tex., spring, 1964); *MCZ 35118 (4:68.0–76.0, Pensacola, Fla.); MCZ 41924 (4:6.7–9.0, 28°51′N, 88°37′W, at surface over 695 m, M/V OREGON Sta. 852, 25 October 1953, 2 CS); MCZ 45015 (10:

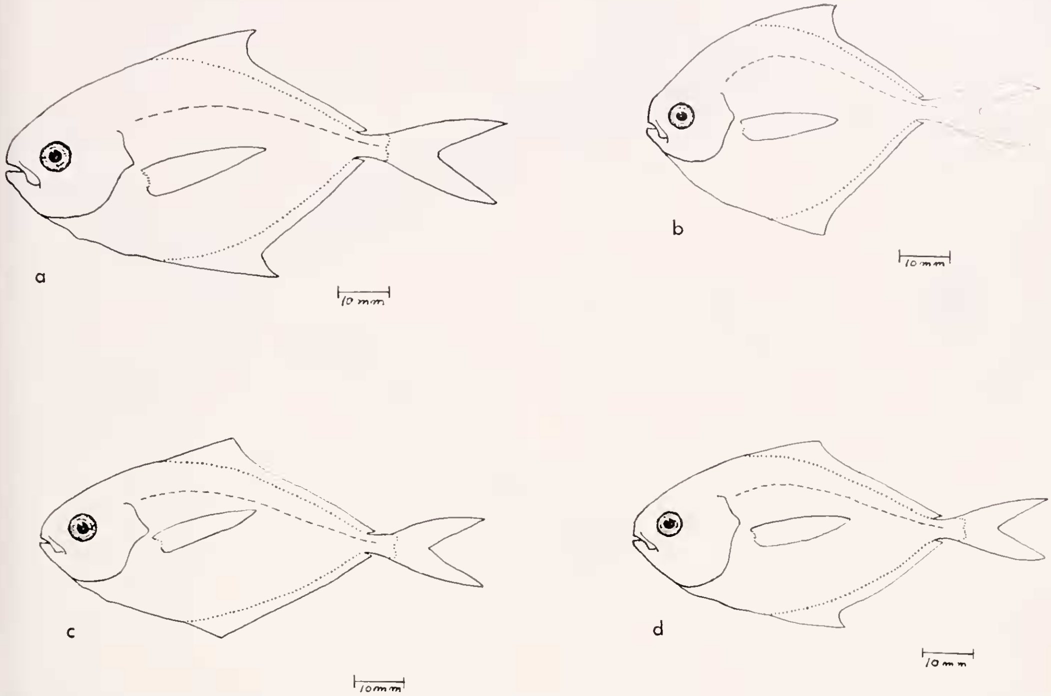


Figure 18. Juveniles of the four Pacific species of *Peprilus*: a = *P. medius*, 77.9 mm SL; b = *P. ovatus*, 60.0 mm SL; c = *P. simillimus*, 71.0 mm SL; d = *P. snyderi*, 66.4 mm SL.

113.5–136.0, 29°45′N, 88°20′W, 37 m, M/V SILVER BAY Sta. 296, 12 March 1958); *MCZ uncat. (22:55.6–102.2, Port Aransas, Tex., 7–20 m, R/V LORENE, 30 June 1967, 16 radiographed); TABL uncat. (1:136.4, 27°04′N, 96°43′W, 82 m, M/V SILVER BAY Sta. 266, 28 January 1958); TABL uncat. (1:133.5, 20°01′N, 91°47′W, 55 m, M/V SILVER BAY Sta. 844, 17 November 1958); TABL uncat. (4:44.0–52.0, Fla., lower Pensacola Bay, between ship channel and south shore from Big Lagoon entrance to U. S. Coast Guard Station, 20 February 1964); TABL uncat. (1:133.7, Fla., 45 miles SW of Pensacola); TU 3979 (3:86.0–104.5, La., Terrebonne Co., Oyster Bayou, 2–4 m, 31 May 1952); TU 4084 (10:38.5–56.2, La., Terrebonne Co., Oyster Bayou 4 m, 12 March 1952); TU 4461 (10:12.5–17.5, La., Jefferson Co., NE end of Grand I., 2–3 May 1952); TU 8945 (7:78.7–122.9, La., Miss. Sound near Grand I. channel, 30°09′N, 89°18′W, M/V ANN INEZ, 26 August 1954); TU 23966 (10: 16.3–30.6, 29°50.5′N, 85°32.5′W, 22 m, M/V OREGON Sta. 2431, 4 March 1959); *USNM 118620 (4:72.0–79.0, Aransas Pass, Tex., 12 May 1940); USNM 147777 (1: 109.0, Miss., 1948); USNM 156116 (1: 100.0, La., Grand I., Barataria Bay, 5 July 1930); *USNM 156118 (2:88.0, 91.0, La., Barataria Bay, 27 November 1951); USNM 156121 (1:97.0, La., Grand I., 5–8 m, 2 July 1930); USNM 156122 (1:97.0, La., Grand I., 21 July 1930); *USNM 156123 (5:94.0–107.0, La., Grand I., 12 miles off Grand Terre, 22 July 1930); *USNM 156124 (1:86.0, Fla., Appalachicola Bay, June, 1932); *USNM 157709 (2:99.0, 100.0, Alabama, 9 m, 29 September 1951); *USNM 159714 (3:56.0–73.0, 30°12.5′N, 88°15′W, Ala., 11 m, M/V OREGON Sta.

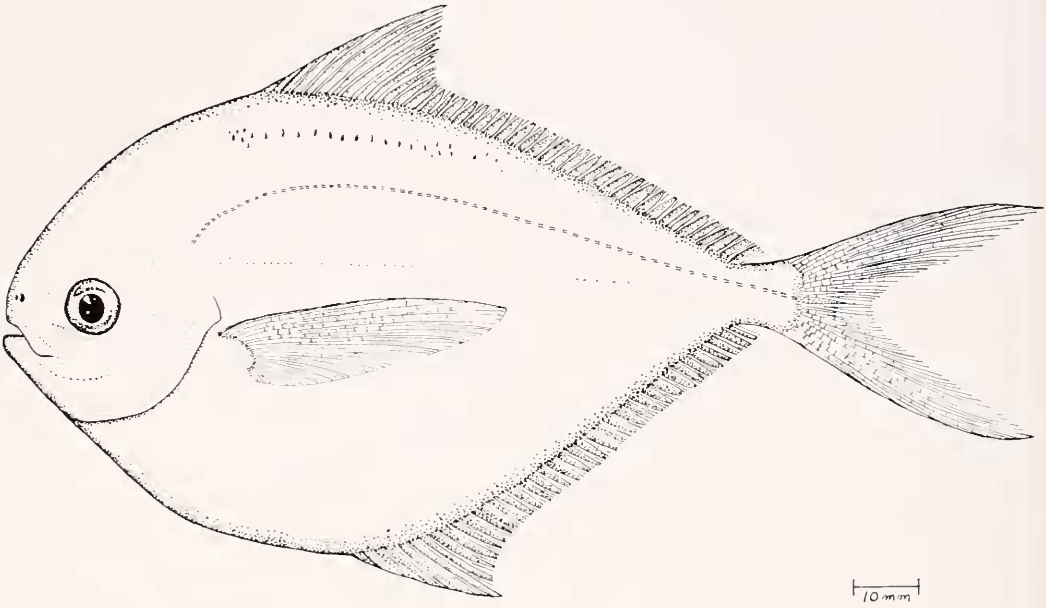


Figure 19. *Peprilus burti*, 113.7 mm SL, Mississippi Sound, 30°09′N, 89°18′W, TU 8945.

2142, 12 March 1958); *USNM 159808 (1:145.0, 28°58′N, 84°44′W, 144 m, M/V SILVER BAY Sta. 154, 22 August 1957); USNM 159825 (1:123.1, 28°30′N, 94°97′W, 35 m, M/V SILVER BAY Sta. 187, 25 September 1957); USNM 163517 (1:143.0, 28°09′N, 84°54′W, 146 m, M/V OREGON Sta. 920, 11 March 1954); *USNM 187922 (4:142.0–167.0, 29°04′N, 85°49′W, 183–186 m, M/V SILVER BAY Sta. 156, 22 August 1957); *USNM 187924 (1:54.2, 29°42′N, 88°40′W, 15–18 m, M/V OREGON Sta. 2193, 25 May 1958); *USNM 187987 (6 meas.:69.0–93.0, 29°07′N, 88°34′W, 229 m, M/V OREGON Sta. 3646, 14 June 1962, 11 radiographed); USNM 188649 (2:103.0, 104.0, 28°47′N, 91°49.5′W, 26 m); USNM uncat. (4:32.0–63.0, 30°09′N, 88°29′W, 13 m, M/V OREGON Sta. 2115, 24 February 1958); *USNM uncat. (3:58.0–76.0, 30°12.5′N, 88°15′W, 11 m, M/V OREGON Sta. 2142, 12 March 1958); *USNM uncat. (31 meas.:53.9–102.1, 30°02′N, 88°42.5′W, 15–17 m, M/V OREGON Sta. 2389, 29 January 1959, 103 radiographed, 2 CS); *USNM uncat. (10:132.0–155.0, Yucatan Peninsula, W of Campeche, 19°42′N, 91°47′W, 49–55 m, M/V SILVER BAY Sta. 1131, 25 April 1959); UMML 750 (4:53.5–68.4, Fla., Appalachicola Bay, 1951); UMML 1804 (1:61.3, Yucatan Peninsula, Campeche, SW of Monas Pt.); UMML 11002 (1:130.8, 28°13.5′N, 92°56′W, 68 m, M/V OREGON Sta. 3804, 14 September 1962); UMML 13268 (1:83.3, 30°07.5′N, 88°42.5′W, 16 m, M/V SILVER BAY Sta. 5006, 22 June 1963); UMML 15813 (1:65.9, 30°07.5′N, 88°43′W, 15 m, M/V SILVER BAY Sta. 5007, 22 June 1963).

Diagnosis. P. burti is a moderately elongate species with slightly falcate dorsal and anal fins. It is distinguished from the closely related *P. triacanthus* by having a deeper body – a mean body depth of 551 compared to 458 for *P. triacanthus*, each in thousandths of SL; 16 or 17 rather than 18 to 20 caudal vertebrae; and, no dark spots along dorsal surface as are frequently present in *P. triacanthus*. The species is distinguished from *P. paru* by having a

TABLE 15. PROPORTIONAL MEASUREMENTS OF *PEPRILUS BURTI*. Symbols as in Table 7. Size range, 7.8–167.0 mm SL; mean size, 79.5 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	216	255–392	303	1.78	8.66
Snout length	215	048–096	069	0.58	12.26
Eye diameter	229	065–144	100	0.97	14.68
Length of upper jaw	215	074–128	089	0.63	10.39
Interorbital width	215	059–131	097	0.65	9.88
Length of pectoral fin	219	228–391	332	3.03	13.49
Predorsal distance I	205	331–529	395	2.59	9.39
Predorsal distance II	215	239–448	292	2.72	13.66
Preanal distance	215	404–582	465	2.38	7.52
Maximum depth of body	232	460–640	551	2.45	6.76
Least depth of caudal peduncle	215	050–096	075	0.52	10.08
In thousandths of HL:					
Snout length	215	167–278	226	1.28	8.31
Eye diameter	216	251–424	328	2.32	10.40
Length of upper jaw	215	200–371	295	1.47	7.33
Interorbital width	214	200–411	319	2.02	9.29

TABLE 16. MERISTIC VALUES OF *PEPRILUS BURTI*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	155	38–48	43.6	0.12	3.53
Anal fin-rays*	155	35–43	39.7	0.11	3.35
Pectoral fin-rays	148	19–23	21.4	0.06	3.59
Total gill rakers	71	21–26	23.3	0.11	3.91
Total vertebrae	273	29–31	30.0	0.01	0.67
Lateral-line scales	4	90–100	–	–	–

* Excluding spines.

row of relatively large pores below the anterior half of the dorsal fin, and by having slightly falcate dorsal and anal fins rather than moderately or extremely falcate ones.

Description. Proportional measurements are given in Table 15 and meristic values in Table 16. Body moderately elongate, moderately deep to deep, compressed; anterior dorsal profile moderately convex. Eye diameter greater than length of snout; eye relatively large. Dorsal and anal fins slightly falcate, longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal fin (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. The system is often very conspicuous in living or freshly collected specimens. There is an irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. Premaxillary teeth slightly recurved, usually with three small cusps. Swimbladder delicate, thin-walled, elongate; found only in specimens smaller than about 100 mm SL. Coloration as described for the genus. Maximum length probably 200 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 6.8 to 14.7 (Table 15) and from 0.7 to 3.9 for meristic characters (Table 16). Comparatively high V values for proportional measurements result partly from some degree of allometry, especially in eye size, and from the inclusion in the sample of a wide size-range of individuals.

The sample size of *P. burti* used (Table

15) is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). The main exception is vertebral number which, as in all the species of *Peprilus,* is relatively constant (Table 5).

Geographic variation. No geographic variation was noted in this species.

Ontogenetic change. Few and moderate changes accompany growth in *P. burti* in a size range of about 8 to 167 mm SL. As shown by ratio-on-size diagrams (Fig. 20), head length, eye diameter, and body depth decrease in size relative to SL with growth, while the relative length of the pectoral fin increases up to about 100 mm SL then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient of the size-on-size regression of eye diameter is relatively low (Fig. 3; Table 6). The size-on-size regressions of body depth for *P. burti* and the closely related *P. triacanthus* (Fig. 2) show the two to be similar in this character up to about 30 mm SL, beyond which size *P. burti* becomes deeper-bodied.

Distribution (Fig. 7). *P. burti* is known only from the Gulf of Mexico. The range extends from the vicinity of Tampa Bay, Florida (about 27°45′N), along the continental shelf to the western side of Yucatan, Mexico (about 21°45′N). Caldwell (1961) lists two records for the species outside of the above range: 1) Big Sarasota, Florida, about 27°30′N, CAS 17237; and 2) Cape Romano, Florida, about 25°54′N, M/V SILVER BAY Sta. 524, the latter based on an unsupported field report. Specimens agreeing closely to the description of *P. burti* are known from shallow water in the Atlantic off Florida. These specimens may represent disjunct members of the species. All such specimens are, however, listed under *P. triacanthus,* the closely related Atlantic Coast species.

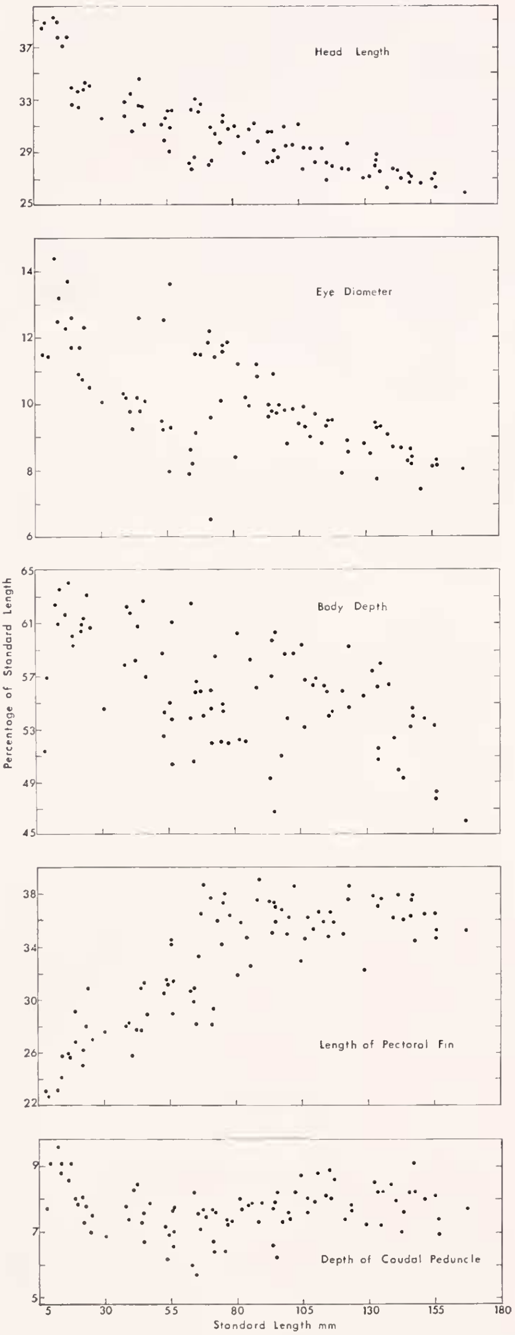


Figure 20. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus burti.*

Taxonomic comments. *P. burti* was originally described as a new species by Fowler (1944) from specimens which he had previously (1933) designated as Gulf of Mexico members of *Poronotus triacanthus.* Fowler (1944) stated that the species was apparently related to *Peprilus palometa* of the Pacific Coast even though he recognized that the former species was different in several respects, including the possession of a row of relatively large pores below the dorsal fin.

P. burti is very closely related to *P. triacanthus* of the Atlantic Coast, a relationship resulting in different interpretations of taxonomic status. Populations in the Gulf of Mexico are frequently referred to as *Peprilus* or *Poronotus triacanthus.* Caldwell (1961) proposed the synonymy of *Peprilus burti* with *Poronotus triacanthus.* Collette (1963), on the basis of differing vertebral counts, considered *P. burti* to be valid. I consider it distinct but close to *Peprilus triacanthus.* The relationships and possible interactions of the two species are discussed on p. 247.

Peprilus triacanthus (Peck, 1804)

Figures 21, 22

Stromateus triacanthus Peck, 1804: 48, fig. 2, pl. 2 (original description, Piscataqua River, New Hampshire, holotype not seen); Günther, 1860: 398; Jordan and Gilbert, 1882a: 451; Jordan and Gilbert, 1882b: 597.

Stromateus cryptosus Mitchill, 1814: 3 (original description, New York Bay, holotype not seen); Mitchill, 1815: 365, fig. 2, pl. 1; Cuvier and Valenciennes, 1833: 408.

Rhombus cryptosus, Cuvier and Valenciennes, 1833: 408.

Peprilus triacanthus, Storer, 1839: 60; Haedrich, 1967: 106, fig. 40.

Rhombus triacanthus, DeKay, 1842: 137, fig. 80, pl. 26.

Poronotus triacanthus, Gill, 1861: 35; Jordan and Gilbert, 1878: 377; Bean, 1880: 91; Jordan and Evermann, 1898: 2849, fig. 405, pl. CL (in part IV); Jordan, Evermann, and Clark, 1930: 267; Bigelow and Schroeder, 1953: 363, fig. 192; Briggs, 1958: 292, in part.

Rhombus (*Poronotus*) *triacanthus,* Jordan and Evermann, 1896: 967, *Poronotus* designated as a subgenus.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). ANSP 11350 (1: 95.6 mm, New Hampshire); ANSP 11353 (1:147.8, Maine); FSBC 1024 (2:81.6, 98.2, Atlantic Ocean, Florida, Duval County, jetty at Atlantic Beach, 29 November 1958); MCZ 2375 (1:185.0, Nahant, Massachusetts); MCZ 16722 (1:197.5, Waquoit, Mass.); MCZ 16745 (1:152.5, Nahant, Mass.); MCZ 16815 (2:118.0, 119.0, Malden, Mass.); MCZ 16822 (1:168.5, Provincetown, Mass.); MCZ 16906 (1:67.0, Eastport, Me.); MCZ 16911 (2:116.5, 120.0, Tarrytown, New York); MCZ 16939 (2: 50.0, 72.0, Penikese I., Elizabeth Is., Mass.); *MCZ 17017 (5:94.5–108.0, Hampton Roads, Virginia); MCZ 17173 (1:195.5, Martha's Vineyard, Mass.); MCZ 17175 (1:164.5, Trenton, New Jersey); MCZ 17207, 17208 (2:138.0, 194.5, Waquoit, Mass.); MCZ 17304 (1:166.5, Cape Cod, Mass.); MCZ 23406 (1:179.0, Nahant, Mass.); MCZ 23928 (1:186.0, New York Harbor, N. Y.); MCZ 25768 (16:10.6–24.6, Newport, Rhode Island, 6 CS); MCZ 34601 (3:57.0–68.0, ALBATROSS II 20852, Mass., 58 m, 14 July 1930); MCZ 34602 (2:26.5, 28.3, Nantucket I., Mass., 24 August 1925); MCZ 42122 (4:7.7–29.7, 39°28′N, 71°10′W, to 39°27′N, 71°26′W, 57 m, R/V ATLANTIS RHB 604, IKMT, 22–23 July 1954, CS); MCZ 42123 (1:113.0, Port Royal, South Carolina); *MCZ 43227 (3:144.0–156.0, Assateague I., Maryland, 10 July 1957); *MCZ 44974 (9:60.0–115.0, Georgia, off Jekyll Island, 25 March 1959, 1 CS); MCZ 44977 (1:121.0, 31°06′N, 79°56.5′W, 46–55 m, M/V SILVER BAY Sta. 5709, 8 May 1964); MCZ 45038 (4:76.5–175.0, Ga., commercial trawling area, 19 August 1959); MCZ 45117 (10:94.5–138.6, Point Judith, R. I., June, 1958); MCZ 45126 (2: 110.2, 121.9, North Carolina, 34°45′N, 76°21′W, 16 m, M/V SILVER BAY Sta.

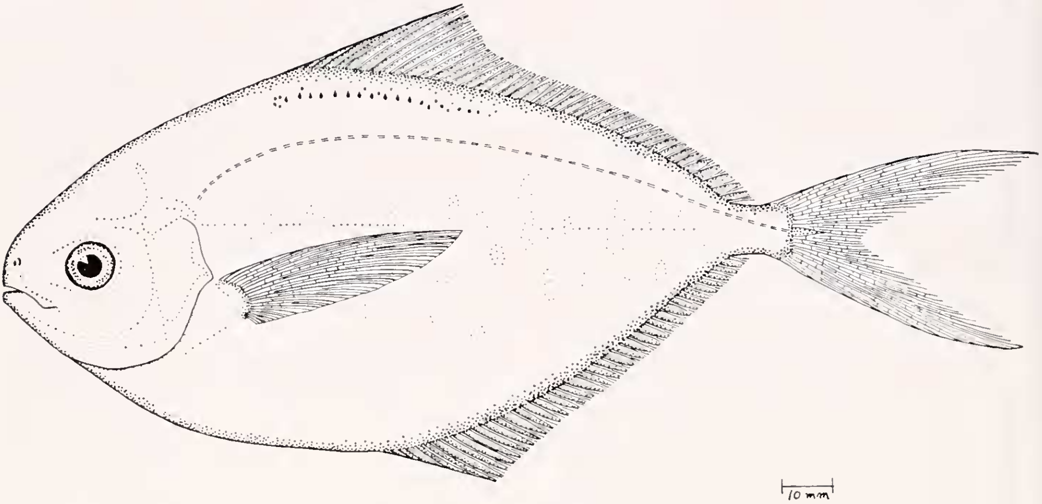


Figure 21. *Peprilus triacanthus*, 157.8 mm SL, fish market, Cambridge, Massachusetts.

1641, 24 February 1960); MCZ uncat. (11:115.0–183.5, Waquoit, Mass.); MCZ uncat. (15:20.5–40.8, E of Long Island, N. Y., 40°46′N, 70°55′W, 5 m, EUGENIE VIII, Cr. 8, Sta. 1, 19–20 August 1961, plankton net on end of longline, 2 CS); *MCZ uncat. (4:122.5–153.0, E of Long I., N. Y., 40°01′N, 71°23′W, bottom to 128 m, CAP'N BILL III, Cr. 65–1, Bait sta. 1, 5 May 1965); *MCZ uncat. (14:106.0–198.0, N. C., 36°30′N, 74°45′W, 110 m, M/V SILVER BAY Sta. 4104, 31 May 1962, 1 radiographed); *TABL 101984 (13 meas.:55.2–138.8, Atlantic Ocean, 30°31′N, 81°22′W, 13 m, M/V SILVER BAY Sta. 3464, 5 October 1961, 17 radiographed); TABL 101990 (1:23.0, Atlantic Ocean, 30°15′N, 80°59′W, 29 m, M/V SILVER BAY Sta. 2795, 7 February 1961, larval trawl); TABL 101991 (1:21.0, Atlantic Ocean, 27°38′N, 80°02′W, 48–57 m, M/V SILVER BAY Sta. 5559, 8 March 1964, nekton net); TABL 101992 (3:9.6–19.8, Atlantic Ocean, 30°46′N, 80°48′W, 25 m, M/V SILVER BAY Sta. 2804, 9 February 1961, larval trawl); TABL 101993 (1:19.0, Atlantic Ocean, 27°43′N, 80°00.5′W, 57 m, M/V SILVER BAY Sta. 5560, 8 March 1964, 1 m, nekton net); TABL 102050 (1:15.0, Atlantic Ocean, 27°21.5′N, 79°57.5′W, 101 m, M/V SILVER BAY Sta. 5551, 7 March 1964); TABL uncat. (1:132.0, Atlantic Ocean, 29°48′N, 80°12′W, 348–366 m, M/V SILVER BAY Sta. 470, 17 June 1958); TABL uncat. (1:119.5, N. C., 34°17′N, 75°55′W, 183–201 m, M/V OREGON Sta. 4973, 29 July 1964); *USNM 311? (1:122.0, Atlantic Ocean, 29°38′N, 80°09′W, 320–329 m, M/V SILVER BAY Sta. 471, 17 June 1958); USNM 156113 (1:72.0, Cape Kennedy, Florida); *USNM 156149 (6 meas.: 54.0–79.0, Fernandina, Fla., March, 1920, 13 radiographed); *USNM 156153 (5:69.0–76.0, Fernandina, Fla., March, 1918); *USNM 158133 (3:116.0–127.0, Atlantic Ocean, 28°03′N, 79°52′W, 274–320 m, M/V PELICAN Sta. 25, 8 April 1956); *USNM 159807 (1:131.0, Atlantic Ocean, 29°15′N, 80°05′W, 384 m, M/V COMBAT Sta. 329, 31 May 1957); USNM 159813 (2:73.0, 79.0, Atlantic Ocean, 30°24′N, 81°22′W, 11–15 m, M/V COMBAT Sta. 504, 2 October 1957); *USNM 159818 (1:61.0, Atlantic Ocean, 29°30′N, 80°11′W, 137 m, M/V COMBAT Sta. 489, 19 August 1957); USNM 159823 (1:75.0, Ga., 31°29′N, 79°33′W, 110 m, M/V COMBAT Sta. 512, 3 October 1957); USNM 188468 (4:

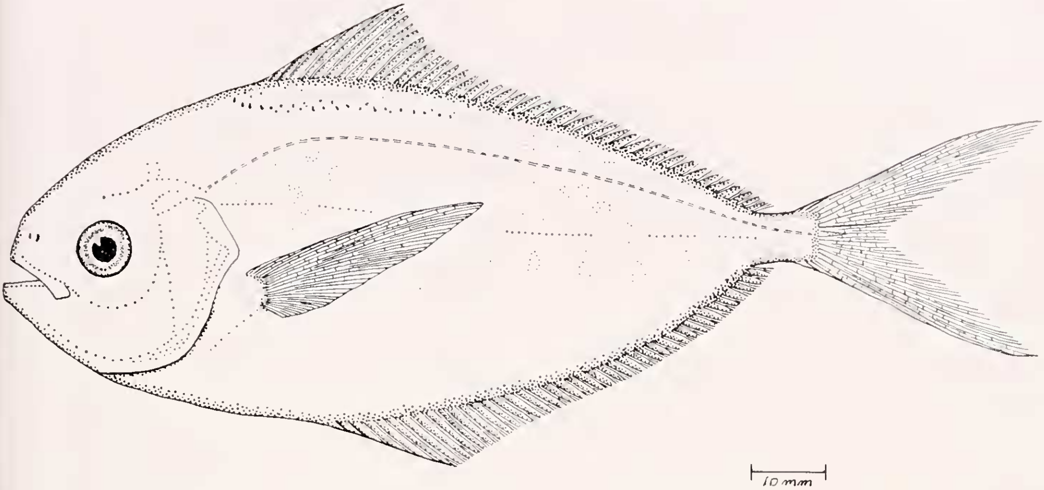


Figure 22. *Peprilus triacanthus*, 122.0 mm SL, off eastern Florida at 320 to 330 m, USNM, SILVER BAY Station 471.

101.0–110.0, Atlantic Ocean 30°39′N, 76°39′W, 229 m, M/V COMBAT Sta. 180, 16 November 1956); *USNM 190367 (10: 61.0–141.0, N. C., 35°01.5′N, 76°02.5′W, 9–15 m, M/V SILVER BAY Sta. 1487, 7 December 1959, 8 radiographed); USNM uncat. (5:95.0–111.0, Delaware, about 15 miles NE of Indian River Inlet, 16 m, 4–5 August 1958); *USNM uncat. (10:133.0–180.0, Atlantic Ocean, 29°45′N, 80°10′W, 329–348 m, M/V SILVER BAY Sta. 489, 21 June 1958, 8 radiographed); *USNM uncat. (4:108.0–132.0, Atlantic Ocean, 29°45′N, 80°20′W, 64–68 m, M/V SILVER BAY Sta. 5687, 1 May 1964); UMML 2479 (1:110.5, Atlantic Ocean, 30°02′N, 80°06′W, 320 m, M/V PELICAN Sta. 49, 12 May 1956); UMML 2924 (1:169.0, Jacksonville, Fla., to Brunswick, Ga., 37–91 m, January, 1956); UMML 4370 (2:105.1, 106.2, N. C., 34°07′N, 76°06′W, 229 m, M/V COMBAT Sta. 175, 15 November 1956); UMML 4497 (1:110.4, Fla., ESE off St. John's River, 1 May 1952); UMML 6937 (2:77.3, 81.7, Atlantic Ocean, St. Augustine, Fla., 7–13 m, 4 August 1960); UMML 7053 (1:111.8, N. C., 34°36′N, 76°13′W, 33–37 m, M/V SILVER BAY Sta. 1643, 24 February 1960); UMML 7340 (10:76.7–98.8, N. C., 34°57′N, 76°03′W, 16–18 m, M/V SILVER BAY Sta. 1631, 23 February 1960); UMML 7614 (1:144.6, S. C., 32°59.5′N, 79°14′W, 9–11 m, M/V SILVER BAY Sta. 1365, 21 October 1959); UMML 8102 (1:64.4, Atlantic Ocean, St. Augustine, Fla., 15–16 m, 29 November 1960); UMML 8527 (1:138.3, Atlantic Ocean, St. Augustine, Fla., 14–15 September 1960); UMML 15049 (1:108.2, Ga., 31°26′N, 79°44′W, 84–102 m, M/V SILVER BAY Sta. 5385, 4 December 1963); UMML 17171 (1:103.0, Ga., 32°01′N, 79°10′W, 137–146 m, M/V SILVER BAY Sta. 5397, 7 December 1963); *UW 13407 (1: 136.6, Gulf of Mexico, NE of Tortugas Light, 12 February 1954, shrimp trawl).

Diagnosis. P. triacanthus is an elongate species with slightly falcate dorsal and anal fins. It is distinguished from *P. paru* by having a more elongate body – mean body depth of 458 compared to 710 for *P. paru*, each in thousandths of SL; a row of relatively large pores below the anterior half of the dorsal fin; and slightly falcate dorsal and anal fins rather than moderately or extremely falcate ones. Characters that distinguish *P. triacanthus* from *P. burti* and *P. simillimus* are listed in the diagnosis

TABLE 17. PROPORTIONAL MEASUREMENTS OF *PEPRILUS TRIACANTHUS*. Symbols as in Table 7. Size range, 10.6–198.0 mm SL; mean size, 102.4 mm SL.

	N	R	x̄	SE	V
In thousandths of SL:					
Head length	182	251–358	289	1.87	8.72
Snout length	182	055–090	071	0.57	10.86
Eye diameter	194	061–133	086	1.12	18.15
Length of upper jaw	182	064–113	085	0.69	10.93
Interorbital width	182	072–111	092	0.62	9.09
Length of pectoral fin	177	179–364	312	2.60	11.06
Predorsal distance I	138	332–492	381	3.23	9.98
Predorsal distance II	182	228–407	278	2.82	13.67
Preanal distance	182	375–544	445	2.23	6.76
Maximum depth of body	203	364–600	458	3.28	10.22
Least depth of caudal peduncle	182	055–089	070	0.54	10.36
In thousandths of HL:					
Snout length	182	175–309	252	1.96	10.49
Eye diameter	182	232–377	292	2.41	11.14
Length of upper jaw	182	239–348	295	1.50	6.87
Interorbital width	182	245–389	320	2.26	9.51

TABLE 18. MERISTIC VALUES OF *PEPRILUS TRIACANTHUS*. Symbols as in Table 7.

	N	R	x̄	SE	V
Dorsal fin-rays*	150	40–48	44.3	0.13	3.63
Anal fin-rays*	152	37–44	40.3	0.11	3.47
Pectoral fin-rays	149	17–22	20.7	0.07	3.96
Total gill rakers	33	22–25	23.8	0.18	4.33
Total vertebrae	279	30–33	31.7	0.03	1.61
Lateral-line scales	9	96–105	–	–	–

* Excluding spines.

of each of these species, respectively. The specific epithet, *triacanthus*, is from the Latin and means "three spines"; it refers to the first dorsal spine, the first anal spine, and the spine on the ventral surface of the pelvic bone, not to the usual presence of three dorsal and three anal spines.

Description. Proportional measurements are given in Table 17 and meristic values in Table 18. Body elongate, shallow to moderately deep, compressed; anterior dorsal profile slightly to moderately convex. Eye diameter greater than length of snout, eye moderately large. Dorsal and anal fins slightly falcate, longest dorsal ray three to five times the length of shortest dorsal ray, longest anal ray two to four times the length of shortest anal ray. Dorsal with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape. The system is often very conspicuous in living or freshly collected specimens. An irregular row of about 17 to 25 relatively large pores just below the anterior half of the dorsal fin. Premaxillary teeth slightly recurved, usually with three small cusps. Swimbladder delicate, thin-walled, elongate, found only in specimens smaller than about 100 mm SL. Dorsal and upper ventral surfaces of the body quite often mottled with large, dark spots; otherwise, coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 6.9 to 18.2 (Table 17) and from 1.6 to 4.3 for meristic characters (Table 18). High V values for proportional measurements indicate considerable variability. Partly it is due to allometry, especially in eye size, and partly to the inclusion in the sample of members of both the shallow and deep-bodied populations from the southern part of the range. Another source of variability, compared to some of the other species, is the inclusion in the sample of individuals of a broad size-range.

The sample size of *P. triacanthus* used (Table 17) is considered to be reasonably adequate, and specimens from all parts of the known geographic range were examined. Ranges of meristic values appear, by inspection, to approach a normal distribution (Tables 1 to 4). The main exception is vertebral number which, as in all the species of *Peprilus,* is relatively constant (Table 5). Variation in vertebral number is slightly higher in this species than in the others and partly due to differences in the two populations in the southern part of the range.

Geographic variation. Two distinct populations apparently exist off the southeastern coast of the United States, one in deep water generally over a mud bottom, and one in shallower water generally over a sand bottom (Table 22). The deep-water fish (Fig. 22) tend to be more elongate with numerous spots on the body and with 18 or 19, usually 19, caudal vertebrae. Those from shallow water tend to be deeper-bodied with no spots and with 17 to 19, rarely 19, caudal vertebrae (similar to *P. burti,* Fig. 19). The *triacanthus–burti* situation is discussed on p. 247.

No other geographic variation was noted.

Ontogenetic change. Few and moderate changes accompany growth in *P. triacanthus* in a size range of about 10 to 198 mm SL. As shown by ratio-on-size diagrams (Fig. 23), head length, eye diameter, and body depth decrease in size relative to SL with growth while the relative length of the pectoral fin increases up to about 100 mm SL, then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient of the size-on-size regression of eye diameter is relatively low (Fig. 3; Table 6).

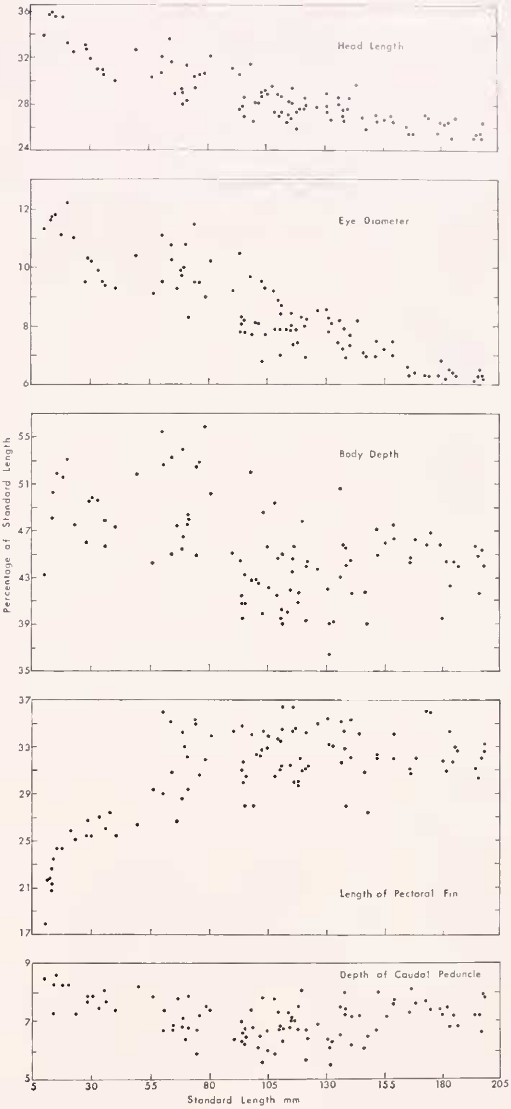


Figure 23. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus triacanthus.*

Distribution (Fig. 7). *P. triacanthus* is known from off the Atlantic Coast of North America from about 48°N in the Gulf of St. Lawrence to about 27°30′N off southern Florida. The species is infrequently collected as far north as the south and east coasts of Newfoundland (Bigelow and Schroeder, 1953), Cape Breton Island (Hoar, 1937), and the outer coast of Nova Scotia (McKenzie, 1939). It occurs in the Gulf of Maine in the summer and autumn. Southward, the species ranges to southern Florida in shallow water (for example, 27°28′N, 80°02′W, 35 m, M/V OREGON Sta. 5319) and to a similar region in deeper water (for example, 28°03′N, 80°29′W, 274–320 m, M/V PELICAN Sta. 25). I have identified one specimen of *P. triacanthus* from the Gulf of Mexico, a male, 136.6 mm SL, from "NE of Tortugas Light" (UW 13407).

Taxonomic comments. Until Haedrich's (1967) revision of the suborder Stromateoidei, the species had been known almost exclusively as *Poronotus triacanthus.* The chief basis for the generic distinction was the presence of a row of relatively large pores below the dorsal fin, a character more reasonably considered as a specific one. For other relevant taxonomic comments, see under *P. burti.*

Peprilus paru (Linnaeus, 1758)

Figures 24, 29

Stromateus paru Linnaeus, 1758: 248 (based on Sloane's (1725) description, Old Harbour, Jamaica, holotype not seen); Jordan and Gilbert, 1882a: 914; Jordan and Gilbert, 1882b: 596; Fordice, 1884: 312.

Chaetodon alepidotus Linnaeus, 1766: 460 (original description, Charleston, South Carolina, holotype not seen).

Rhombus alepidotus, Lacépède, 1800: 321.

Sternoptyx gardenii Bloch and Schneider, 1801: 494 (original description, Carolina, holotype not seen (after Linnaeus)).

Stromateus longipinnis Mitchill, 1815: 366 (original description, New York Bay, holotype not seen).

Seserinus xanthurus Quoy and Gaimard, 1824 (original description, Rio de Janeiro, Brazil, holotype not seen); Fowler, 1906: 119.

Peprilus crenulatus Cuvier, 1829: 214 (original description, locality ?, holotype not seen); Cuvier, 1836–1849: 141, fig. 3, pl. 64.

Rhombus longipinnis, Cuvier and Valenciennes, 1833: 401, pl. 274; DeKay, 1842: 136, fig. 239, pl. 74.

Rhombus argentipinnis Cuvier and Valenciennes, 1833: 405 (original description, Montevideo, Uruguay, holotype not seen).

Rhombus xanthurus, Cuvier and Valenciennes, 1833: 405; Jordan and Evermann, 1898: 2849.

Rhombus crenulatus, Cuvier and Valenciennes, 1833: 410, pl. 275.

Peprilus longipinnis, Cuvier, 1836–1849, fig. 2, pl. 63 (in Atlas by Valenciennes); Gill, 1861: 35.

Stromateus gardenii, Günther, 1860: 399.

Rhombus orbicularis Guichenot, 1866: 245 (original description, Cayenne, French Guiana, holotype not seen).

Peprilus alepidotus, Goode, 1879: 112; Goode and Bean, 1879: 130; Bean, 1880: 92; Bigelow and Schroeder, 1953: 368; Briggs, 1958: 292; Springer, 1961: 482; Haedrich, 1967: 106, fig. 41.

Stromateus alepidotus, Jordan and Gilbert, 1882a: 451; Jordan, 1884: 149; Bean and Dresel, 1884: 156.

Rhombus (*Rhombus*) *paru,* Jordan and Evermann, 1896: 965, *Rhombus* a genus and a subgenus.

Rhombus (*Rhombus*) *xanthurus,* Jordan and Evermann, 1896: 966, *Rhombus* a genus and a subgenus.

Rhombus paru, Jordan and Evermann, 1898: 2849, fig. 404, pl. CL (in Part IV).

Peprilus paru, Evermann and Marsh, 1900: 141, fig. 39; Meek and S. F. Hildebrand, 1925: 411; Jordan, Evermann, and Clark, 1930: 266; Briggs, 1958: 292; Haedrich, 1967: 106.

Seserinus paru, Fowler, 1916: 402; Fowler, 1942: 152.

Sesserinus xanthurus, Fowler, 1942: 152 (error in spelling of generic name; referable to *Seserinus xanthurus* Quoy and Gaimard, 1824).

Simobrama xanthura, Fowler, 1944: 3, fig. 2.

Material examined. Those specimens marked with an asterisk (*) have been radiographed. The number radiographed equals the number measured unless otherwise indicated. CS indicates specimens cleared and stained. Size ranges, in mm, are standard lengths (SL). FSBC 306 (1:63.6 mm, Gulf of Mexico, Florida Keys, 24°41′–52′N, 82°00′–35′W, 14–15 January 1958); FSBC 1745 (2:90.9, 95.5, Gulf of Mex., Fla., Pinellas Co., Johns Pass, Madeira Pass, 25 April 1960); FSBC 2282 (4:75.1–83.8, Mississippi, Horn I., 27 October 1962); FSBC 2572 (1:71.0, Gulf of Mex., Fla., 27°43′N, 82°45′W, 24 February 1963); FSBC 2562 (6:65.6–95.9, Gulf of Mex., Fla., 27°43′N, 82°45′W, 19 December 1962); FSBC 3831 (2:92.0, 138.0, Gulf of Mex., Fla., Tampa Bay, 1 mile S of MacDill AFB, 23 January 1966); FSBC 3956 (3:74.0–149.0, Gulf of Mex., Fla., Pinellas Co., 27 December 1966); IMS 325 (1:63.0, near Pass Cavallo, Texas, 6–11 m, 22 October 1960); IMS 326 (1:106.7, Tex., 18 miles W of Sabine, 12 m, 15 June 1951); IMS 333 (2:42.5, 54.0, Tex., Mustang I., 6–7 m, 21 October 1950); IMS 1019 (1:68.3, near Port Aransas, Tex., 10 July 1962); IMS 1178 (1:137.0, 50 miles E of Port Aransas, Tex., 57–58 m, 6 December 1961); IMS uncat. (9:21.2–61.2, near Port Aransas, Tex., spring, 1964); LACM 4489 (2:61.5, 69.3, Mayagüez, Puerto Rico, October, 1963, 1 CS); *LACM 4988 (1:175.0, Mayagüez, P. R., March, 1964, beach seine); *LACM 4989 (1:172.0, Mayagüez, P. R., March, 1964, beach seine); *LACM 5725 (1:103.7, Jamaica, Kingston market); *LACM 6741–21 (1:70.0, Mayagüez, P. R., 8 December 1966); *LACM 7884 (1:103.3, Mayagüez, P. R., 9 February 1963); MCZ 1687 (1:75.0, Beaufort, North Carolina); MCZ 4600 (1:118.0, Brazil); MCZ 16778 (1:106.0, Brazil); MCZ 16999 (1:73.0, Fla.); MCZ 17104 (2:123.0, 141.0, Rio de Janeiro, Brazil); MCZ 17129 (2:132.0, 137.0, Pensacola, Fla.); MCZ 17336 (1:123.0, Fla. Keys); MCZ 17364 (1:131.0, Penikese I., Elizabeth Is., Mass.); MCZ 26291 (1:106.0, Mobile, Alabama); MCZ 41064 (2:47.4, 56.3, Port au Prince, Haiti, August, 1950); *MCZ uncat. (5:112.0–148.5, Port Aransas, Tex., 6–7 m, 3 July 1967, tide trap, 2 radiographed); MCZ uncat. (1:60.0, N. C., Bogue Sound, August, 1966, CS); *SU 2774 (3:124.3–140.0, Washington market); *SU 4900 (2:136.9, 168.6, Jamaica); *SU 14025 (1:222.0, Argentina, Buenos Aires market, 1934); *SU 38704 (3:76.5–80.6, Aransas Pass, Tex., 12 May 1940); *SU 51811 (2:98.7, 105.5, Recife, Brazil, 23 November 1944); *TABL 101976 (1:137.8, Honduras, off Caratasca Lagoon, 15°49.5′N, 83°44′W, 31 m, R/V UNDAUNTED Cr. 6703, 7 April 1967); *TABL 101977 (7:115.7–130.1, Honduras, off Caratasca Lagoon, 15°54′N, 83°40′W, 37 m, R/V UNDAUNTED Cr. 6703, 8 April 1967); *TABL 101978 (2:85.4, 103.6, Honduras, off Caratasca Lagoon, 15°45′N, 83° 32′W, 33–37 m, R/V UNDAUNTED Cr. 6703, 9 April 1967); *TABL 101979 (1:132.4, Honduras, off Caratasca Lagoon, 15°56′N, 83°41′W, 37–40 m, R/V UNDAUNTED Cr. 6703, 12 April 1967); *TABL 101980 (2:102.9, 107.5, Honduras, off Caratasca Lagoon, 15°19′N, 83°26′W, 9 m, R/V UNDAUNTED Cr. 6703, 10 April 1967); *TABL 101982 (3:84.8–96.5, Honduras, off Caratasca Lagoon, 15°21′N, 83°34′W, 9 m, R/V UNDAUNTED Cr. 6703, 10 April 1967); *TABL 101983 (2:114.8, 123.0, British Honduras, Belize, 17° 12′N, 88°11.2′W, 18–20 m, R/V UNDAUNTED Cr. 6703, Sta. 72, 18 May 1967); *TABL uncat. (2:106.2, 134.9, Guyana, about 8°45′N, 59°15′W, 29 m, M/V CALAMAR Sta. 72, 18 June 1967); *TABL uncat. (7:82.2–97.7, Guyana, about 7°N, 58°30′W, near mouth of Essequibo River, M/V CALAMAR Sta. 82, 20 June 1967); *TABL uncat. (6:56.4–121.2, Surinam, about 6°N, 55°30′W, 20 m, M/V CALAMAR Sta. 102, 15 July 1967); *TABL uncat. (1:88.1, Surinam, about 6°N, 54°30′W, 20 m, M/V CALAMAR Sta. 100, 14 July 1967); *TABL uncat. (1:104.2, Surinam, about 6°N, 54°30′W, 27–29 m, M/V CALAMAR Sta. 121, 11 August 1967); *TABL uncat. (2:113.9, 154.2 Surinam, about 6°N, 54° 30′W, 22–24 m, M/V CALAMAR Sta. 84, 21 June 1957); *TABL uncat. (3:78.5–90.4, Surinam, about 6°N, 54°30′W, 16–18 m, M/V CALAMAR Sta. 133, 15 August 1967); TABL uncat. (1:45.6, Georgia, Jekyll I. beach, 19 July 1956); TABL uncat. (1:62.6, Ga., commercial trawling area, 16 January 1957); TABL uncat. (1:100.2, Ga., commercial trawling area, 6 July 1959); TABL uncat. (2:80.6, 115.4, Ga., commercial trawling area, 12–18 July 1959); TABL uncat. (4:50.7–108.0, Ga., commercial trawling area, 26–30 July 1959); TABL uncat. (3:61.3–85.7, Ga., commercial trawling area, 6 August 1959); TABL uncat. (1:177.0,

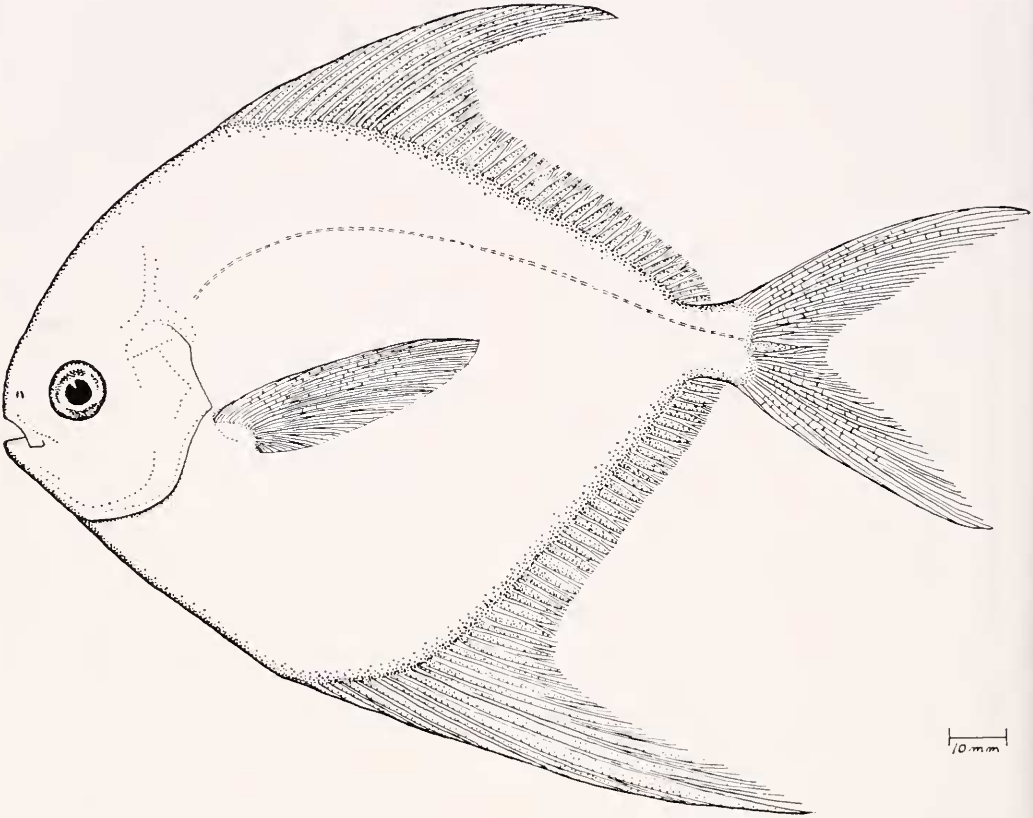


Figure 24. *Peprilus paru,* 126.8 mm SL, Port Aransas, Texas, MCZ uncatalogued.

Trinidad, Port of Spain market, M/V OREGON, 26 September 1964); TABL uncat. (2:146.0, 172.0, Venezuela, 9°32′N, 60°24′W, 60 m, M/V OREGON Sta. 2348, 20 September 1958); TABL uncat. (2: 140.0, 146.0, off Campeche, Mexico, 20° 01′N, 91°47′W, 55 m, M/V SILVER BAY Sta. 844, 17 November 1958); TABL uncat. (1:68.4, N. C., 33°57.5′N, 77°50.5′W, 11 m, M/V SILVER BAY Sta. 1666, 27 February 1960); TABL uncat. (5:67.4–76.3, South Carolina, 32°55.5′N, 79°29′W, 9 m, M/V SILVER BAY Sta. 5423, 11 January 1964); TABL uncat. (1:135.8, Atlantic Ocean, Fla., 28°04′N, 80°11.5′W, 27–29 m, M/V SILVER BAY Sta. 5513, 29 February 1964); *TU 4396 (10:57.6–101.5, Louisiana, Terrebonne Co., mouth of Oyster Bayou, 31 October 1952); TU 9224 (10:25.5–33.1, La., Lake Pontchartrain, 2 miles SE of south draw, 30°10′N, 89°55′W, 11 August 1954); *USNM 3083 (3:50.0–63.0, Plum Point, Maryland, 22 August 1949); *USNM 30064 (1:153.0, Jamaica); *USNM 63660 (1:147.0, P. R., San Juan market); *USNM 63655 (1:114.0, Tex., Matagorda Bay); *USNM 83362 (2:93.0, 94.0, Rio de Janeiro, Brazil); *USNM 86716 (1:131.0, Uruguay); *USNM 117650 (1:152.0, Paraguay ?); *USNM 118637 (6:118.0–140.0, Galveston, Tex., 2 June 1940, 4 radiographed); *USNM 123044 (3:66.0–68.0, Golfo de Venezuela, Piedras Bay, 14 March 1925, USS NIAGARA); *USNM 156134 (8:55.0–93.0, Aransas Pass, Tex., GRAMPUS Sta. 10476); *USNM 158505 (10:115.0–155.0, Tex., E of Padre I., 27°32.5′N, 96°28′W, 60 m, M/V OREGON Sta. 4, 25 May 1950); UMML 187 (1:155.0, Belize, British Honduras, 17°10′N, 88°18′W, 27 September 1956); UMML 2085 (1:87.7, Dry Tortugas, 24°45′–50′N, 82°10′–30′W, 1955–1956); UMML 8271 (1:57.3, Atlantic Ocean, St. Augustine, Fla., 21 December 1960); UMML 12422 (1:93.0, French Guiana, 5°48′N, 52°53′W, 44 m, M/V OREGON Sta. 4190, 22 February 1963); UMML 13462 (1:60.8, Atlantic Ocean, St. Augustine, Fla., 1 February 1961); UMML 13986 (1:86.5, Surinam, 6°16′N, 55°56′W, 27 m, M/V OREGON Sta. 4171, 19 February 1963); UMML 16374 (1:49.2, Gulf of Mex., Fla., Okaloosa Co., 9–10 September 1963); UMML 16817 (2:18.2, 25.7, Fla., Monroe Co., Everglades Natl. Park, Shark River Delta, 5 November 1964); UMML 17068 (1:142.5, Colombia, 9°35′N, 76°04.5′W, 40–55 m, M/V OREGON Sta. 4895, 26 May 1964); UMML 21799 (2:99.5, 102.4, Golfo de Venezuela, 11°46′N, 71°16′W, 24 m, M/V OREGON Sta. 5670, 6 October 1965); UMML 21812 (2:30.3, 50.1, Golfo de Venezuela, 11°27′N, 71°39′W, 27 m, M/V OREGON Sta. 5673, 6 October 1965); UMML 22232 (1:110.0, Colombia, 8°48′–46.8′N, 76°39.7′–42.8′W, R/V PILLSBURY Sta. 360, 12 July 1966); WHOI 66264B (1:83.0, Carmen, Mex., about 18°N, 92°W, 15 March 1950).

Diagnosis. P. paru is a very deep-bodied species with moderately to extremely falcate dorsal and anal fins. The longest rays of each fin are six or more times the length of the shortest rays of each fin. Characters that distinguish *P. paru* from *P. burti, P. triacanthus,* and the related *P. medius* are listed in the diagnosis of each of these species, respectively. The specific epithet, *paru,* is a Brazilian name used by Linnaeus (1758) following Sloane's (1725) designation of the species as "Paru pisci Brasiliensi Congener."

Description. Proportional measurements are given in Table 19 and meristic values in Table 20. Body ovate, very deep, compressed; anterior dorsal profile moderately to strongly convex. Eye diameter greater than length of snout; eye relatively large. Dorsal and anal fins moderately to extremely falcate, longest dorsal and anal rays six or more times the length of shortest dorsal and anal rays; anterior anal rays often extremely long, as much as 20 to 25 times the length of shortest ray. Dorsal fin with two to four (usually three) small spines preceding the rays; anal with two or three (usually three) small spines preceding the rays. Base of anal fin slightly shorter than base of dorsal (fewer rays). Caudal fin long to very long, deeply forked, about 25 to 35 per cent of total length. Subdermal canal system usually indistinct in preserved specimens, seen as vertical, parallel lines on body and dendritic canals on top of head and nape; pores very small on body and usually not visible except in small individuals. Premaxillary teeth slightly recurved, pointed, simple. Swimbladder delicate, thin-walled, elongate; found only in specimens smaller than about 100 mm SL. Coloration as described for the genus. Maximum length probably 280 mm SL.

Variation. Coefficients of variation (V) for proportional measurements range from 5.8 to 14.5 (Table 19) and from 0.6 to 5.1 for meristic characters (Table 20). Relatively high V values indicate considerable variability and are partly due to: allometry, especially in eye size; the inclusion of a wide size-range of individuals in the sample; and, to irregular variation over the broad geographic range of the species.

Meristic characters other than vertebral number and gill raker number vary more than in the other species of the genus (Tables 1 to 5). Dorsal, anal, and pectoral fin-ray numbers vary geographically and are discussed below.

Geographic variation. P. paru occurs along the Atlantic Coast of the United States from Chesapeake Bay or just northward to Florida, in the Gulf of Mexico, in the West Indies, along the coast of Central

TABLE 19. PROPORTIONAL MEASUREMENTS OF *PEPRILUS PARU*. Symbols as in Table 7. Size range, 18.2–222.0 mm SL; mean size, 94.3 mm SL.

	N	R	$\bar{x}$	SE	V
In thousandths of SL:					
Head length	182	251–396	305	1.93	8.54
Snout length	195	044–084	062	0.56	12.63
Eye diameter	202	058–147	103	1.05	14.46
Length of upper jaw	182	065–112	084	0.68	10.90
Interorbital width	182	085–144	112	0.84	10.14
Length of pectoral fin	196	274–454	386	2.51	9.11
Predorsal distance I	182	369–503	435	2.12	6.57
Predorsal distance II	179	258–399	319	2.02	8.48
Preanal distance	182	369–636	484	3.27	9.13
Maximum depth of body	205	565–877	710	4.25	8.57
Least depth of caudal peduncle	191	066–112	092	0.58	8.66
In thousandths of HL:					
Snout length	182	148–247	204	1.41	9.35
Eye diameter	182	228–442	334	2.35	9.51
Length of upper jaw	182	233–318	275	1.19	5.82
Interorbital width	182	245–479	368	1.74	6.37

TABLE 20. MERISTIC VALUES OF *PEPRILUS PARU*. Symbols as in Table 7.

	N	R	$\bar{x}$	SE	V
Dorsal fin-rays*	178	38–47	42.9	0.12	3.75
Anal fin-rays*	176	35–45	40.4	0.14	4.73
Pectoral fin-rays	172	18–24	21.9	0.09	5.11
Total gill rakers	98	20–23	21.5	0.07	3.12
Total vertebrae	182	29–31	30.0	0.01	0.57
Lateral-line scale	22	80–95	–	–	–

* Excluding spines.

America, and along the coast of South America, rather abundantly to Rio de Janeiro, and less commonly to Argentina. After the publication of "The Marine Fishes of Panama" by Meek and S. F. Hildebrand (1925), Hildebrand (MS) stated that there were two distinct species among the populations of *P. paru:* 1) *P. alepidotus* from the Atlantic Coast of the United States and the Gulf of Mexico; and 2) *P. paru* from the West Indies, Central America, and South America. He noted that *P. paru* differed from *P. alepidotus* in having a more robust body, larger scales, and slightly shorter (fewer rays) dorsal and anal fins, particularly the anal. Hildebrand also stated that while each has an equal number of pectoral rays, *P. paru* has a narrower pectoral and a less falcate dorsal fin than *P. alepidotus.* His findings were based on numerous specimens from the United States, two from the West Indies, two from Panama, five from Venezuela, four from Brazil, and five from Uruguay.

Following Hildebrand's analysis, *P. paru* and *P. alepidotus* have been considered distinct in faunal and fishery works.

Based upon the examination of 207 specimens from throughout the species range, I find only partial agreement with Hildebrand's conclusions. Although body proportions do vary, I could not detect geographic variation of characters reflecting the "robustness" of the body, nor could I find decided differences in the size of the scales or in the shape of the pectoral fin. Some slight differences may exist in the above three characters but do not seem of sufficient magnitude to warrant distinction. Contrary to Hildebrand's statement that the dorsal fin of *P. alepidotus* is more falcate than that of *P. paru,* I find that the length of the anterior lobes of both dorsal and anal fins tends to increase in a north-to-south direction. This follows a general trend existent in a number of fish groups – that the fins are longer in more

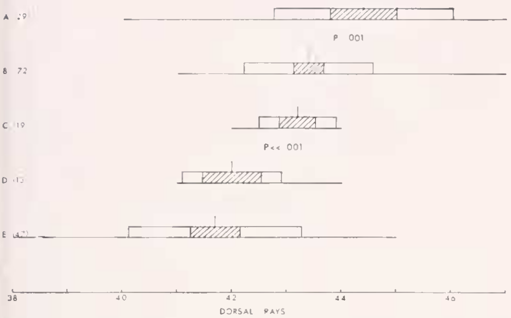


Figure 25. Geographic variation in the number of dorsal fin-rays of *Peprilus paru*: A = United States, Atlantic Ocean; B = Gulf of Mexico; C = Central America; D = West Indies; E = South America; numbers in parentheses are sample sizes. The horizontal line represents the range of values; the vertical line represents the mean; the large, hollow rectangle represents one standard deviation on either side of the mean; the small, barred rectangle represents the 95 per cent confidence interval. Each P value is for comparison of the two sample means immediately above and below the value; only P values of 2 per cent or less are listed.

tropical waters (Frederick H. Berry, personal communication). In *P. paru* it appears to be partly an individual variation since certain fish from a single sample may have extremely falcate dorsal and anal fins.

The counts of the dorsal, anal, and pectoral rays vary geographically, but in each case the variation is clinal rather than being a basis for dividing the populations into two distinct species. The clines are in an irregular north-to-south pattern and are diagrammed in Figures 25 to 27 in a manner generally following the method of Hubbs and Hubbs (1953).

The number of dorsal rays shows a regular gradient in the manner in which I have arranged the regions (Fig. 25) although, in a strictly latitudinal sense, the positions of the West Indies and Central America should probably be reversed. The ranges of values overlap widely, but in proceeding from one coastal region to another in a north-to-south direction, the sample from the United States Atlantic shows a significant difference from the

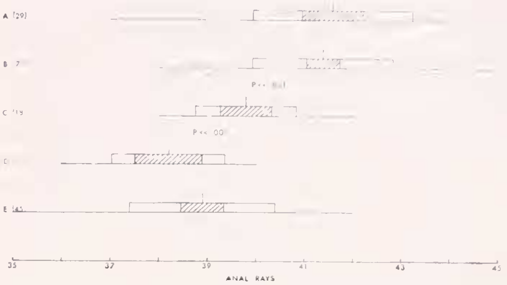


Figure 26. Geographic variation in the number of anal fin-rays of *Peprilus paru*. Explanation of symbols in Figure 25.

Gulf of Mexico sample, and the Central American population has a significantly different number from the West Indian and the South American populations. The levels of significance were set at the 2 per cent level using a two-tailed Student's *t*-test.

The greatest difference among populations of the five regions occurs in the number of anal fin-rays, although the ranges of values overlap considerably (Fig. 26). In this character the United States Atlantic and Gulf of Mexico populations are very similar. The latter sample differs significantly from the Central American sample and in turn the Central American one is

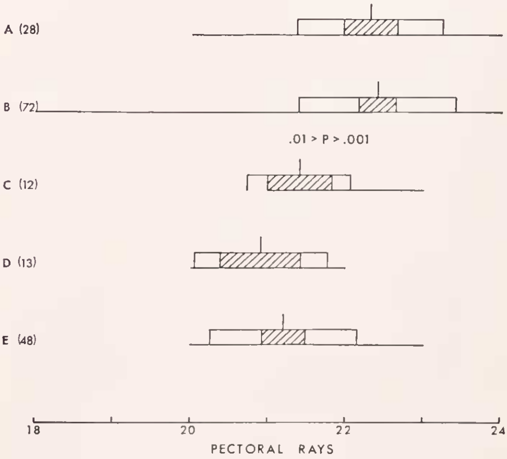


Figure 27. Geographic variation in the number of pectoral fin-rays of *Peprilus paru*. Explanation of symbols in Figure 25.

significantly different at the 2 per cent level from the West Indian sample. The Central American sample is different from the South American one, but only significant at the 2 to 5 per cent level. The West Indian members are the most aberrant among the five regions; however, the sample size (13) is the smallest. The differences in this character among the regional populations do not seem strong enough to suggest a subspecific designation, especially since other characters vary in a different manner.

In the pectoral ray number the gradient is slight, the overlap is considerable, and there is less difference among the populations than in the above two meristic characters (Fig. 27). The Central American population is significantly different from the Gulf of Mexico member, but the southern populations are completely contained in the ranges of values of the United States Atlantic and Gulf populations.

Further evidence for divergence among the populations of *P. paru* has come from an examination of the parasitic isopods which inhabit the gill chambers of this species. Thomas E. Bowman (personal communication) has found that the cymothoid isopods taken from United States Atlantic and Gulf populations are different from those taken from *P. paru* collected off Surinam. The species in the former regions is *Lironeca ovalis* Say (possibly a synonym of *L. redmanni* Leach), while those from the Surinam specimens are very similar in some ways but in other characters are different enough to possibly be considered as members of a distinct species. Specimens from the intermediate areas, West Indies and Central America, are needed to clarify the status of the populations. It may be that the isopods are geographically varying in a manner parallel to their hosts. If there are two species of isopods involved, this would lend support to the recognition of two separate species among the populations of *P. paru.* It would not be conclusive evidence since it is to be expected that rates of differentiation and speciation would be different in the two animal groups.

In summary, there is apparently semi-isolation and some differentiation among regional populations of *P. paru.* Although there is probably no complete break in gene flow, it does appear to be reduced, the reduction effected by barriers of deep water and unfavorable coastlines. *P. paru* is essentially a shallow-water species and would cross deep water only infrequently, probably most commonly by passive transport of eggs and larvae. The species is most abundant in areas where the continental shelf is broad and with large expanses of shallow water. Zones where the shelf is narrow or where the shore is rocky may serve as partial barriers to *P. paru.* Although the distribution of *P. paru* is continuous around Florida, it is uncommon in southern Florida; and there is evidence of slight differentiation between Atlantic and Gulf populations (Fig. 25). Atlantic and Gulf populations differ more significantly in the three meristic characters discussed above from West Indian forms than from the Central American ones. This disparity may be partly due to the gap of deep water separating the United States from the West Indies as compared to continuous coastline from the Gulf to Central America. Some differentiation is apparent between Gulf and Central American populations and may be effected somewhat by the lack of favorable coastlines between the two regions. The West Indian form appears to be most similar to South American members of the species. Continuity and genetic interchange are probably being maintained between these two regions via the shallow coastal areas associated with the chain of West Indian islands. Deep water and unfavorable coastlines are apparently serving to partially isolate Central American populations from the West Indian and South American populations, respectively.

Mayr (1963: 361) states that clines are the product of two conflicting forces:

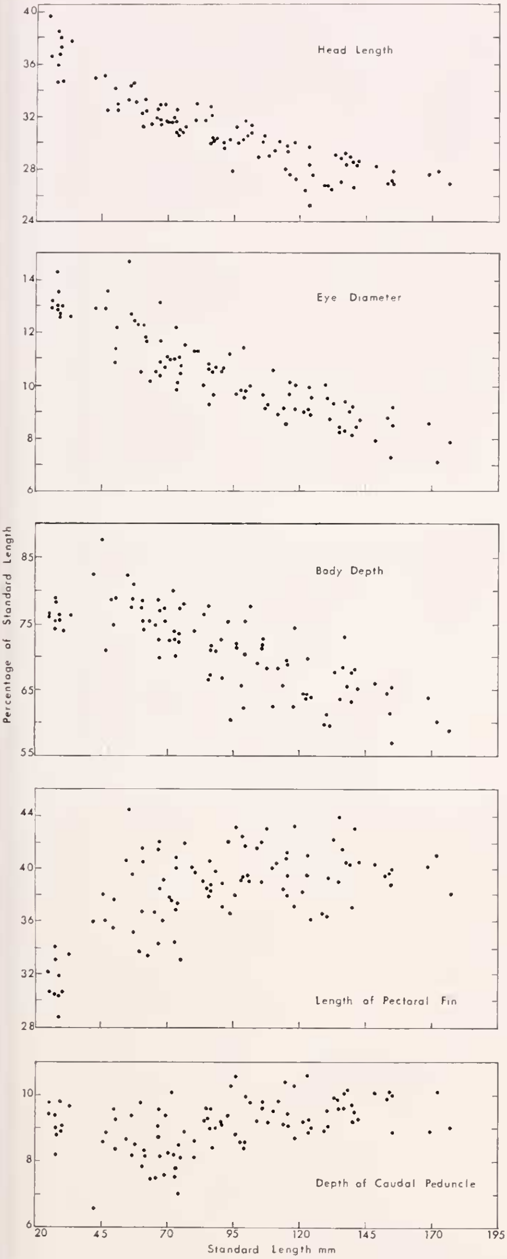


Figure 28. Ratio-on-size scatter diagrams for five morphometric characters of *Peprilus paru*.

selection, which would make every population uniquely adapted to its local environment; and, gene flow, which would tend to make all populations of a species identical.

Mayr (1963: 365) further states that in many cases gene flow seems responsible for the maintenance of clines to a greater degree than environmental gradients. The cohesive effect of gene flow seems to be exceedingly potent. Although a temperature gradient is probably partially responsible for the clines in characters of *P. paru*, it seems that gene flow between contiguous populations is of equal or greater importance. If temperature were of prime importance, an increase in meristic values in the extreme southern portion of the species range might be expected. I have not found such a pattern.

Ontogenetic change. Few and moderate changes accompany growth in *P. paru* in a size range of about 25 to 177 mm SL. As shown by ratio-on-size diagrams (Fig. 28), head length, eye diameter, and body depth decrease in size relative to SL with growth, while the relative length of the pectoral fin increases up to about 100 mm SL then becomes nearly constant; the relative depth of the caudal peduncle remains nearly constant. The correlation coefficient in a size-on-size regression for eye diameter is relatively low (Fig. 3; Table 6).

Distribution (Fig. 7). *P. paru* is known from Chesapeake Bay or just north on the Atlantic Coast of the United States southward around peninsular Florida to throughout the Gulf of Mexico, Central America, and at least part of the West Indies to South America where it commonly occurs to about 23°S in the vicinity of Rio de Janeiro, Brazil, and less abundantly as far south as Argentina. The species infrequently ranges as far north as Long Island and rarely as far as the Gulf of Maine, the most northerly capture being at Cape Elizabeth, Maine, about 43°N (Bigelow and Schroeder, 1953). *P. paru* has been collected near a number of West Indian Islands including Jamaica, Puerto Rico, Haiti, and Trinidad.

Taxonomic comments. Since the descriptions by Linnaeus of *Stromateus paru* in 1758 and *Chaetodon alepidotus* in 1766, the taxonomic status of the species has been in question. Various names have been applied to this widely-distributed and variable species; hence, the synonymic list is an extensive one.

It has become customary in faunal and fishery works to list *P. alepidotus* as the species along the Atlantic and Gulf coasts of the United States and *P. paru* as the species along the West Indies, Central and South America. *P. paru* is the name sometimes given to the Gulf of Mexico populations, and *P. alepidotus* to the population off the Atlantic Coast of the United States. Briggs (1958) lists both as occurring off the Atlantic and Gulf coasts of the United States; this seems to be the least likely situation. In this study, all populations are included within *P. paru.*

Lütken (1880) listed a fish he called *Stromateus paru* as occurring at the southern end of the Strait of Malacca between Malaya and Sumatra in southeast Asia. His drawing was of a small fish which had pelvic fins. *P. paru* is restricted to the New World and has no pelvic fins. Therefore, this species is excluded from being the fish of Lütken's description. Lütken's drawing may be referable to *Parastromateus* (= *Apolectus*) *niger*, a fish representing a monotypic family of uncertain affinity.

P. paru is commonly known as the "harvestfish." Names less frequently used are "starfish" and "poppyfish."

ASPECTS OF FUNCTIONAL MORPHOLOGY

Information on the morphology and ecology of the members of the genus *Peprilus* is sufficient to allow some interpretations of functional morphology, and differences among the species are great enough to allow consideration of some trends and specializations which appear to be developing. It is instructive to see whether certain trends correspond to those thought to be occurring generally in perciform fishes.

Skeletal features. Ossification of various parts of the skeleton of *Peprilus* appears to occur differentially. Study of cleared-and-stained material of two species, *P. triacanthus* and *P. burti,* shows that the vertebral column is ossified very early. Specimens of 6 or 7 mm SL have the anterior two-thirds of the column almost completely ossified, while the posterior one-third and the hypural plate are in the early stages of ossification. In these same specimens the bones of the head are incompletely ossified; the pectoral girdle is apparently relatively well ossified and the pectoral fin is short and fanlike; the jaw teeth and the teeth of the pharyngeal sac have formed; and the dorsal and anal fins are almost completely absent at this stage. In specimens of 8 to 10 mm SL the epural elements remain unossified while the hypurals are more completely ossified; the median fins, particularly anteriorly, are beginning to ossify. In specimens of 12 to 18 mm SL the rays of the median fins are visible and all parts except the epurals are near complete ossification (stromateids do not have strongly ossified skeletons). The caudal skeleton has by this size range achieved a higher degree of symmetry with the hypural plate occupying a more equal position dorsally and ventrally, and with the urostyle becoming more slender; the epurals have reached almost complete ossification and the caudal fin has begun to fork. In the smallest specimens examined (5 mm SL) the hypural plate had the same degree of fusion as in the adult skeleton – two epural and four hypural elements. At a size range of 25 to 30 mm SL the epurals are ossified and the pectoral fin has become more elongate. No differences in pattern of ossification between the two species were found.

The pattern of ossification may correlate with the behavior of the young fish. Spawning occurs offshore generally, and the young are in the pelagic surface layers of the ocean. After hatching, and until several days after the yolk sac is absorbed, the larvae are essentially planktonic with probably little locomotor effort of their own. Early vertebral ossification results in a supporting element of some rigidity. Also, the pectoral fins appear early at about four or five days in *P. triacanthus* (Colton and Honey, 1963). As the caudal apparatus and the median fins strengthen through ossification, and as the caudal fin becomes forked, the young fish becomes more independent in locomotion and at a size of 10 to 15 mm SL probably becomes more nektonic than planktonic. The juvenile fish frequently become associated with coelenterate medusae or siphonophores at a size of 10 to 30 mm SL.

Fishes of the genus *Peprilus* and the family Stromateidae in general have deep, compressed bodies, which are deepest in the region of and just posterior to the body cavity. All seven species of *Peprilus* are similar osteologically, and one of the most conspicuous skeletal regions is that surrounding the body cavity and supporting the viscera. This "visceral basket" gives obvious support and protection to the viscera and abdomen. It is formed anteriorly and ventrally by the cleithrum and the large, posteroventrally directed pelvic bones which unite posteriorly to form a single structure. The vertebrae and pleural ribs house the body cavity dorsally. Posteriorly, the enlarged first interhaemal swings posteriorly to meet the haemal spine of the first caudal vertebrae. The pair of elongate postcleithra provide lateral support. An increased number of anal finrays in the stromateids has apparently resulted in the angular position of the first interhaemal.

While most meristic characters of species of *Peprilus* vary considerably, the vertebral number varies only slightly (Table 5). No geographic variation in vertebral number was detected in any of the species, with the possible exception of the complex *burti-triacanthus* situation off the Atlantic coast of the southeastern United States. Variation is so slight that the vertebral count becomes an important specific character in this genus. For the seven species, 1255 vertebral counts were made. Coefficients of variation (Tables 8, 10, 12, 14, 16, 18, and 20) are very low for this character, indicating great homogeneity within a species.

Several authors (Hubbs, 1926; Vladykov, 1934; Tåning, 1952; Bailey and Gosline, 1955; and others) have shown that meristic elements, including vertebrae, are influenced by temperature and that the number of such elements is progressively greater to the north, or at higher altitudes, or in locally colder areas of spawning. Variation in vertebral number in certain fish groups is often so great that the character must be used only with caution, as has been shown by Bailey and Gosline (1955) for darters of the family Percidae. But in *Peprilus* variation is slight and vertebral number is an important distinguishing character. The caudal vertebrae of *Peprilus* vary more than the precaudal ones, a situation found to be a somewhat general one by C. L. Hubbs (1922). It may be that precaudal vertebrae are fixed earlier in development than most other meristic characters, as is true in the paradise fish, *Macropodus opercularis* (Lindsey, 1954).

Constancy of vertebral number may be correlated with certain other characters involved in evolutionary trends. Bailey and Gosline (1955) have stated that in the family Percidae decreased size is apparently, and probably casually, correlated with reduction in vertebral number. Increase in attenuation within the Percidae appears to be primarily or entirely associated with the elongation of the vertebral centra, rather than with an increase in vertebral number; deepening of the body is marked by some foreshortening of the vertebrae. Barlow (1961) reacted skeptically to the idea that the addition or subtraction of a few elements would be of selective value. However, as in the Percidae, vertebral number in the species of *Peprilus* seems to be significantly associated with size and body shape (Table 21). Size of individual vertebrae seems to be about the same among the species.

P. snyderi, the most elongate and probably the largest species in the genus, has the greatest number of vertebrae, 36. *P. paru*, the deepest-bodied of the species, and also considered to be the most highly derived member of the genus, has the fewest vertebrae, 29 to 31. The close relative of *P. paru* in the Pacific, *P. medius*, is a more elongate species and has 33 to 35 vertebrae. *P. ovatus*, the deep-bodied, small derivative of *P. medius*, has 31 to 33 vertebrae. The relatively elongate *P. triacanthus* has 31 to 33 vertebrae while its close but slightly deeper, smaller relative, *P. burti*, has 29 to 31. The only exception to the trend occurs in *P. simillimus*, a relatively elongate species, which has 30 or 31 vertebrae. Vertebral number in association with other character trends appears to have selective value in the genus, and this selection apparently reduces the variability of the character.

In stromateoid evolution the general tendency has been toward an increase in the number of vertebrae (Haedrich, 1967). This trend seems to have culminated in the rather high number among the Stromateidae. However, from the basal stromateid stock the trend in *Peprilus* seems to be toward a reduction in number of vertebrae in correlation with the trend toward a deep, less elongate body.

Body form; shape, position, and loss of fins. Body form is associated with the shape and position of the fins and both in turn are associated with the locomotion and mode of life of the fish. Myers (1958), Liem (1963), and Patterson (1964) have stated and presented evidence that within the teleostean fishes and particularly the acanthopterygians there has been a trend toward a shorter, deeper, more highly compressed body. Associated with this trend have been several changes in skeletal features and in the shape and location of the fins.

The Stromateidae represent the zenith of stromateoid evolution (Haedrich, 1967) and are among the smallest fishes of the suborder. Within the Stromateidae, particularly the genus *Peprilus*, a number of specific conditions and trends exemplify some of the general tendencies occurring in acanthopterygian fishes.

All species of *Peprilus* are relatively deep, varying from elongate to very deep, and are highly compressed. A trend in spiny-rayed fishes has been for the pectoral fins to move to a lateral position on the body and for the pelvic fins to migrate forward from an abdominal position. The pectoral fin in a lateral position has assumed the primary functions of braking and turning (Harris, 1937; Patterson, 1964). The braking movements of the pectoral produces a lift as well as a drag force. Harris (1937) has shown that the neutralization of this lift force is effected by an equal downward force produced by the anteriorly-placed pelvic fins. If migration of the pelvics had not occurred in evolution along with the migration upward of the pectorals, the fish would either tilt upwards or rise bodily when it comes to a stop.

Extension of a pectoral facilitates turning; and turning is most rapid if the mass is concentrated at the level of the pectorals, the fulcra in turning (Patterson, 1964). Such a concentration of mass can be achieved by deepening the body, and for retention of streamlined form, greatest depth is required about at the level of the pectoral.

The dorsal and anal fins function to stabilize against rolling motion, i. e., they serve primarily as keels (Breder, 1926; Harris, 1937). A fish inclined to roll will do so about the long axis of the body; thus, for the dorsal and anal fins to be most effective they need to be as far as possible from the long axis. If the body is deepened, the dorsal and anal fins are farther from the long axis, and rolling stability is increased.

That the pelvic fins act as bilge keels has been advocated by Breder (1926). Harris (1937) differs and states that the pelvics may be used rather to produce rolling movements for establishing equilibrium or for swimming between rocks or into crevices in other than an upright position.

The swimming behavior of adults of three species, *P. triacanthus*, *P. burti*, and *P. paru*, was observed in this study. In each instance the fishes were accustomed to the tank and locomotion was apparently normal. All species were observed in public aquaria or in tanks in which I had placed freshly collected fish. Swimming appears to be a continuous process with no hovering in midwater. Locomotion is partially produced by the usual serial contractions of myomeres, but propulsion by the flapping of the pectoral fins is also well developed, especially at less than maximum speeds. Fishes of this genus appear to be moderately rapid swimmers with the ability for quick turning and for continuous swimming for long periods of time.

Pelvic fins are present in only one species of the Stromateidae, in specimens smaller than 100 mm SL of *Stromateus fiatola* (Haedrich, 1967). Other stromateoids have pelvic fins that are generally situated under the pectorals; the pelvics are very large in *Nomeus*. The loss of pelvic fins might seem to be a major evolutionary change. A rather specific geometric and hydrodynamic condition of the body in relation to swimming and mode of life of the fish should exist or develop if a species or group of species can dispense with a set of paired appendages. In S. *fiatola* the pelvics are apparently in the process of being lost, and in the other stromateids these fins have already been lost. In several groups of perciform fishes pelvic fins are quite small and in some they are absent. The actual form of the pelvic fins appears to be of little significance in rapid swimming, these fins being no more than maneuvering devices and often following the form of the pectorals. The pelvics are the fins most commonly modified so as to lose all locomotor function. The following discussion considers the loss of the pelvics only in the stromateid fishes, but may also apply to certain other perciform groups.

The position and function of the pectorals, the shape of the body, and the mode of swimming all should be relevant to the loss of the pelvics. In *Peprilus* the pectorals appear to perform at least three functions: braking, turning, and propelling. Propulsion is of the carangiform type, supplemented by the synchronous flapping of the pectoral fins. The latter is more important at lower speeds. This use of the pectorals is common in short, deep-bodied forms, according to Breder (1926).

Breder stated that with the development of a short, deep, compressed body, and a centrally-located pectoral, may come a reduction or loss of pelvic fins – as in the genus *Vomer* (Carangidae) or in *Peprilus triacanthus*. *Vomer* is a deep, extremely compressed pelagic fish with very small pelvics which seem, certainly, to be of little functional importance. *P. triacanthus* is also a deep, highly compressed pelagic fish, the adults of which swim continuously without hovering. If frequent braking does not occur, as seems to be the case in *Peprilus*, less of a downward force is needed or less frequently needed to counteract the lift force created by the pectorals in braking. Also, the deep portion of the body beneath the pectorals should provide some downward force which would further reduce the need for pelvic fins. Breder reasoned that the pelvics may be large, as in the somewhat primitive perciform genus, *Lepomis* (Centrarchidae), which frequently stops and hovers.

Fishes of the genus *Peprilus* appear to possess several attributes for moderately rapid swimming at least for short periods. The caudal fin is deeply forked. Gero (1952) has demonstrated that the tips of the caudal fin produce less turbulence than the center portion. Thus, the more deeply forked the fin, the less should its oscillations disturb the water. As the aspect ratio (= (span of the fin)^2/area of the fin) is increased the drag diminishes. Aspect ratios of *Peprilus* range from about 3.5 in *P. simillimus* to about 5.0 or more in *P. medius*, which puts the group into the upper range or above of Nursall's (1958) category of "typical fish." This category includes fish which have moderate amplitude and fairly high frequency waves to form swimming oscillations, a flexible vertebral column of 24 to 100 vertebrae, a definitely narrowed but muscular caudal peduncle, and a flexible, forked tail of intermediate aspect ratio (two to four).

Breder (1926) stated that pectorals of spatulate or fanlike form accompany fishes of slow or moderate speeds, while long and falcate ones accompany rapid swimmers. The rapid swimmers were said to use such fins largely for quick-turning and seldom, if ever, for either propulsion or for maintaining a stationary position. The above does not agree with the condition in *Peprilus* in which the pectorals of large juveniles and adults are long and winglike, but are used in propulsion.

One function of the dorsal and anal fins is to produce stability against rolling (Breder, 1926; Harris, 1937). The cross section of many fish, including *Peprilus*, is elliptical at the level of the pectoral fins (Fig. 29). The corresponding position of maximum tangential velocity during rolling movements are not at the sides, but at the top and the bottom of the body, the positions of the dorsal and anal fins. The dorsal and anal fins of rapidly swimming fish are often somewhat similar in size and shape, especially in the latter. Frequently in less active forms, one fin may be larger than the other. A trend or at least a morphological arrangement mentioned by Breder (1926) which seems to be operative in *Peprilus* is that in reasonably elongate forms that have the pelvic fins greatly reduced or wanting, the anal fin is usually quite long with the vent displaced forward and the first interhaemal directed backward. Another observation of Breder which seems to have some relevance in the genus *Peprilus* is that of the relation of the development of the dorsal and anal fins to the area of concentration of the bulk of the body. Breder (1926) observed that in fishes with their greater bulk above a line from the tip of the snout to the middle of the peduncle, the dorsal fin is generally larger than the anal. And conversely, when the bulk is below that line, the anal fin is generally the larger. In fishes nearly symmetrical about such a line, the dorsal and anal fins are nearly equal in size. Five species of *Peprilus, P. snyderi, P. simillimus*

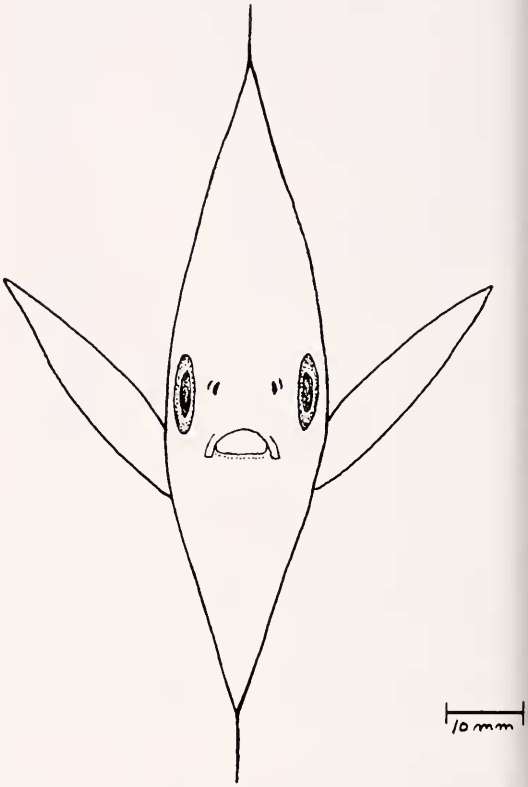


Figure 29. Frontal view of *Peprilus paru*, 117.0 mm SL specimen.

mus, P. triacanthus, P. burti, and *P. medius*, have the greater bulk above the line and all have dorsal fins which are longer (more rays) than the anal fins (Table 21). *P. paru* has slightly greater bulk above the line and has only a slightly longer dorsal than anal fin (Table 21), while the anal is usually more falcate. *P. ovatus* is nearly symmetrical about this longitudinal line and, in turn, the dorsal and anal fins are very similar in size and shape (Table 21); the mean ray counts are about equal (D, 42.8; A, 43.0). The above pattern suggests that selection favors the size and positioning of these steadying keels which provide the optimum range of stability. The extremely long anterior lobes of the dorsal and anal fins of *P. paru* and *P. medius* may serve to increase rolling stability in these deep-bodied fishes, and the anal lobes may somewhat replace the pelvic fin in producing a downward force in counteraction to the upward force produced by the pectoral fin.

Patterson (1964) has stated that during teleost evolution the number of precaudal vertebrae has been reduced more drastically than the number of caudal vertebrae. This feature is characteristic of stromateoid fishes. The results of this change in proportion, according to Patterson, is that in acanthopterygian fishes the less muscular abdominal region is reduced more than the highly muscular and propulsive caudal region, and the resistance to lateral oscillation of the anterior part of the fish is reduced. These trends can be compensated for by increasing the depth of the trunk, for the streamlined form of the fish demands that the greatest depth be anterior to the point of contraction in oscillating the tail. The most elongate species, *P. snyderi*, has 15 precaudal and 21 caudal vertebrae; the shorter, deeper species of *Peprilus* have 13 precaudal and as few as 16 caudal vertebrae.

Swimbladder and mode of life. Changes in the mode of life during development are probably closely correlated with the size and shape of the pectoral fins and with the state of the swimbladder.

The larvae and small juveniles of *Peprilus* are surface dwellers after hatching in offshore waters. They then generally migrate to coastal waters and bays. At a length of about 10 to 30 mm SL, the young frequently become associated with jellyfish medusae and may maintain such a relationship up to a size of 80 to 100 mm SL. This association is well documented (Pearson, 1941; Bigelow and Schroeder, 1953; Mansueti, 1963; and others), and appears to be an important aspect of the life history.

The young fish apparently seek protection among the coelenterate tentacles and also feed on the tentacles themselves. Mansueti (1963) has shown in laboratory experiments that the association requires of the fishes an ability to hover, a locomotor attribute not evident in adult *Peprilus*. The adults that I have observed (three species) swim continuously with little or no hovering in midwater.

Two characteristic changes seem to correlate with the above apparent shift in habit and locomotor pattern. The first is the change of the pectoral fin from a short, fanlike structure to a long, winglike one. The change begins early and continues until the fish reaches a size of 80 to 100 mm SL (Figs. 9, 11, 15, 17, 20, 23, and 28). The second change is the apparent regression of the swimbladder in individuals larger than 80 to 100 mm SL. Although the information is from only three species, *P. triacanthus, P. burti*, and *P. paru*, a swimbladder is present in these fishes up to at least a size of about 100 mm SL. The organ is elongate, thin-walled, and slightly inclined anteriorly. In adult specimens of all species no swimbladder has been found, although fresh or well-preserved material of every species has not been examined. It seems, then, that the swimbladder becomes regressed and nonfunctional in fishes larger than 100 mm SL. It may be that the swimbladder is functional in juveniles and important in hovering and maintaining position

TABLE 21. ASSOCIATIONS AND TRENDS OF CERTAIN CHARACTER VALUES AMONG THE SPECIES OF *PEPRILUS*. The deepest-bodied species is listed at left followed in order of decreasing body depth by the other species. Mean morphometric values are in thousandths of SL.

	paru	*ovatus*	*burti*	*medius*	*simillimus*	*triacanthus*	*snyderi*
Body depth	710	619	551	529	461	458	427
Preanal distance	484	481	465	434	440	445	424
Predorsal distance I	435	408	395	390	369	381	364
Caudal peduncle depth	092	079	075	078	065	070	071
Eye diameter	103	093	100	082	073	086	070
Pectoral fin length	386	360	332	386	336	312	329
Mean total vertebrae	30.0	32.0	30.0	34.0	30.2	31.7	36.0
Ratio of dorsal rays to anal rays	1.04	1.00	1.10	1.06	1.13	1.10	1.11
Relative length of anterior lobes of median fins*	1	3	4	2	6	4	5

* Longest lobes given rank of 1.

under floating objects such as jellyfish medusae, and that the organ becomes nonfunctional when swimming becomes continuous.

Jordan and Evermann (1896) indicated that the swimbladder is "usually" absent in stromateid fishes. Breder (1926), in discussing the hydrostatic situation for fishes which lack a swimbladder, stated that some fishes such as *P. triacanthus* (indicating that this fish has no swimbladder) are so close to the specific gravity of water due to a sufficient amount of fat, that only the slightest movement suffices to keep them from sinking or rising. Fishes of this genus are quite oily and perhaps this condition does facilitate the maintenance of position and the ease of ascent or descent. I have observed the movements of adult *P. triacanthus* in aquaria, and it appears that slow sinking follows cessation of active swimming, but that only the slightest pectoral movements return the fish to a horizontal or an upward direction. H. F. Taylor (1922) calculated that absence of a swimbladder in other than bottom forms should occur only in marine fishes since the quantity of fat necessary to float a fish in the less dense fresh water is practically prohibitive. He estimated that a marine fish with a fat content of 29.34 per cent and with no swimbladder would be in equilibrium with sea water. Many other factors, however, including the relative amount and density of bone need to be considered in this situation.

N. B. Marshall (personal communication) states that a number of shallow-water marine fishes have regressed, age-dependent swimbladders. He includes in the list certain gobies, blennies, flatfishes, certain *Solenichthys* spp., most muraenid eels, gadids such as *Gaidropsarus* spp., and some percomorphs such as *Thalassoma bifasciatum*, *Holacanthus tricolor*, *Upeneus prayensis* and an oceanic species, *Nomeus gronovii*. The latter species is a stromateoid and lives closely associated with the siphonophore, *Physalia*. Whether *Nomeus* stays with *Physalia* all its life is uncertain. The familiar small, blotched *Nomeus* found under *Physalia* may only be the young form of a bigger fish which lives in deep water. In *Nomeus*, as in *Peprilus*, regression of the swimbladder may correlate with a change in mode of life.

The above discussion of swimbladder loss is speculative at this stage. A number of questions remain to be resolved. Further examination of specimens, observations of living fish, and a series of experiments are being planned in an attempt to answer some of the questions. A comparative study of stromateoids and other fishes with

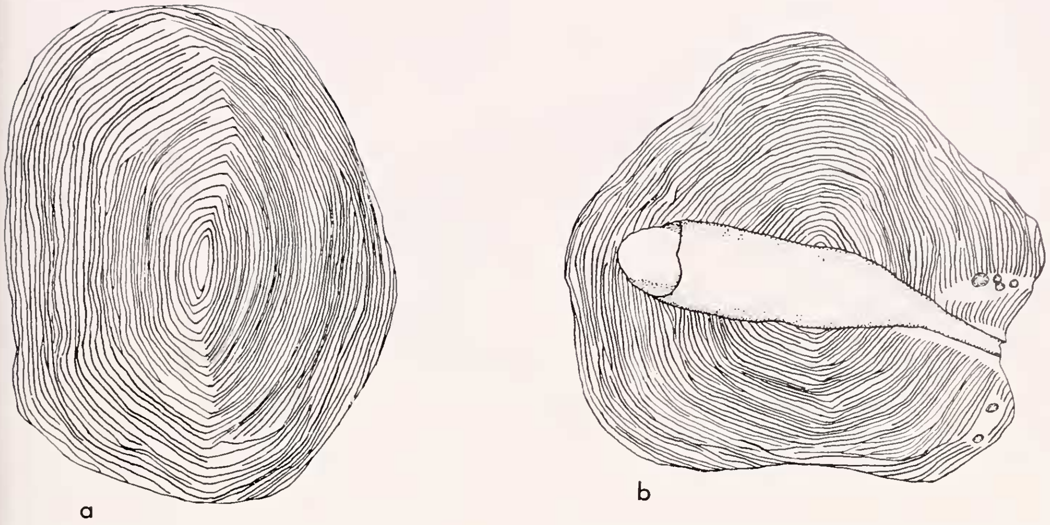


Figure 30. Scales of *Peprilus snyderi*: a = scale from trunk below lateral line; b = lateral line scale from mid-trunk region. From 227.0 mm SL specimen.

regressed, age-dependent swimbladders is being initiated.

Character associations. Listed in Table 21 are the mean values of some morphometric and meristic characters which illustrate trends in sets of characters among the species of *Peprilus*. *P. paru*, the shortest, deepest-bodied species, is listed first in the table, followed in order by the more elongate species. From this ranking the table shows how other characters relate to that of body depth. Greatest body depth is associated with the greatest preanal and predorsal distances, the longest pectoral, the largest eye, and the fewest vertebrae. In the most elongate species, *P. snyderi*, these character values are largely reversed. *P. snyderi* probably does not have the quick-turning ability attained by *P. paru* or *P. ovatus*, for example.

I have not analyzed unit characters or their roles by the techniques of Olson (1964), although this approach might be instructive, especially if applied to the entire suborder.

Skin and scales. The skin of *Peprilus* is thin and, as in most other stromateoid fishes, the scales (Fig. 30) are thin, cycloid, irregular in shape, highly deciduous, and in shallow pockets in the skin. The lateral line scales (Fig. 30b) have a simple tube passing through the middle, and are less deciduous than scales of other parts of the body. The scale condition in *Peprilus* may be important in achieving greater maneuverability and may represent a stage in a trend toward complete loss of scales. The cephalic lateral line consists of pores and branching canals on the cheek, opercular area, snout, lower jaw, and top of head.

In the stromateoid fishes there is usually a well-developed subdermal canal system which communicates to the surface through small pores scattered over the head and body (Haedrich, 1967). The system is particularly well developed in *Peprilus* (Fig. 31), and is conspicuous in living or freshly collected fish. The canals often are only slightly visible after preservation. There are some differences in the system among the species of the genus. *P. burti* and *P. triacanthus* (Fig. 19 and 21–22) have a row of large pores beneath the anterior half of the dorsal fin. A series of

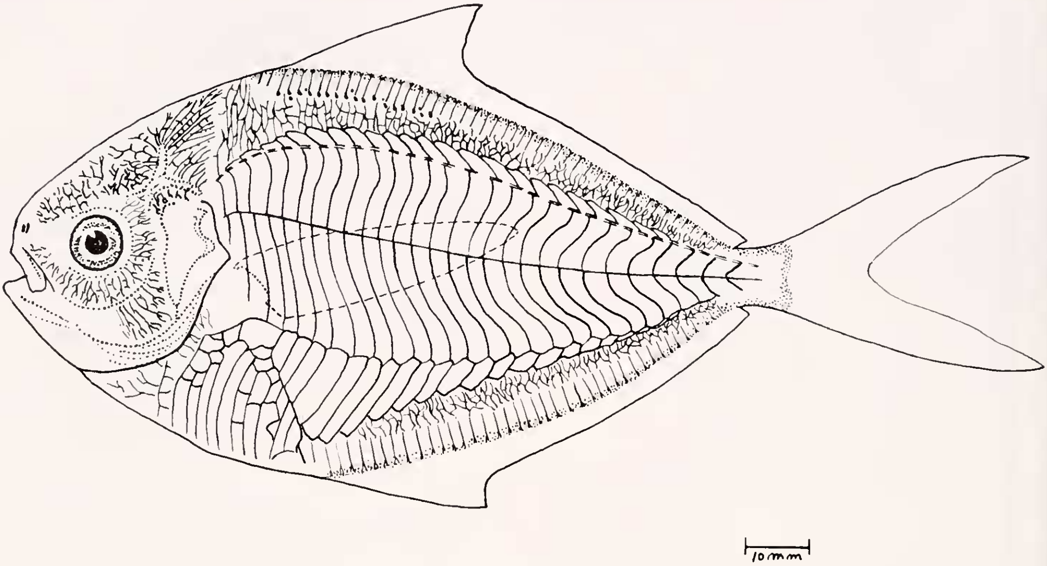


Figure 31. Subdermal canal system and portions of the cephalic lateral line of *Peprilus burti*, 124.6 mm SL specimen.

small, irregularly-spaced, but conspicuous pores are sometimes evident along the dorsal surface of *P. ovatus* (Fig. 10).

The function of this extensive canal system is unknown. Whether the system is independent of the lateral line and whether sensory structures are present are unknown. If the canals contain a sensory mechanism, they may function as receptors important in the formation and maintenance of schools. These fishes produce large amounts of mucous, and the system might be used in the dispersal of the mucous which may contain an agent that counteracts coelenterate toxins. Walters (1963), in a study of the integument and subdermal canal system of the trachipterid fishes, has proposed that the canal system functions in boundary-layer control through distributed dynamic damping. Such control could apparently decrease drag by 60 to 75 per cent. According to the hypothesis, as the skin pressure mounts beneath a growing boundary-layer perturbation, the layer will sink through the surface pores to enter the subdermal canals; the canal fluid will simultaneously flow toward regions of lower pressure and re-enter the boundary layer through the surface pores. This simultaneous series of events would dynamically damp the disturbance. Walters also found similar integuments in two species of Gempylidae. LaMonte (1958) reported that the skin of marlin, genus *Makaira*, has many minute, round openings. Whether such a system operates in *Peprilus* or in gempylids and marlin is unknown. Metabolic economy in *Peprilus* does not seem critical, and selection pressure for such a mechanism would not appear to be great. However, all the above possibilities as to function remain in question, and further investigation is required.

Alimentary canal. The alimentary canal with its several elaborations (Fig. 32) suggests that feeding and food conversion are rather specialized. Each part of the canal is considered below, and an attempt is made to correlate the part with its probable function.

The jaw teeth (Fig. 33) are small, uni-

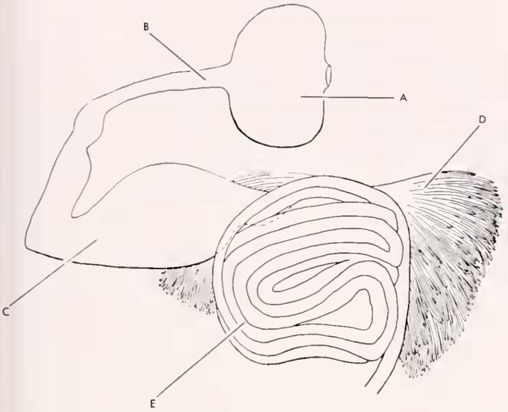


Figure 32. Alimentary canal of *Peprilus paru*: A = pharyngeal sac; B = esophagus; C = stomach; D = pyloric caeca; E = intestine. From 124.6 mm SL specimen (semidiagrammatic).

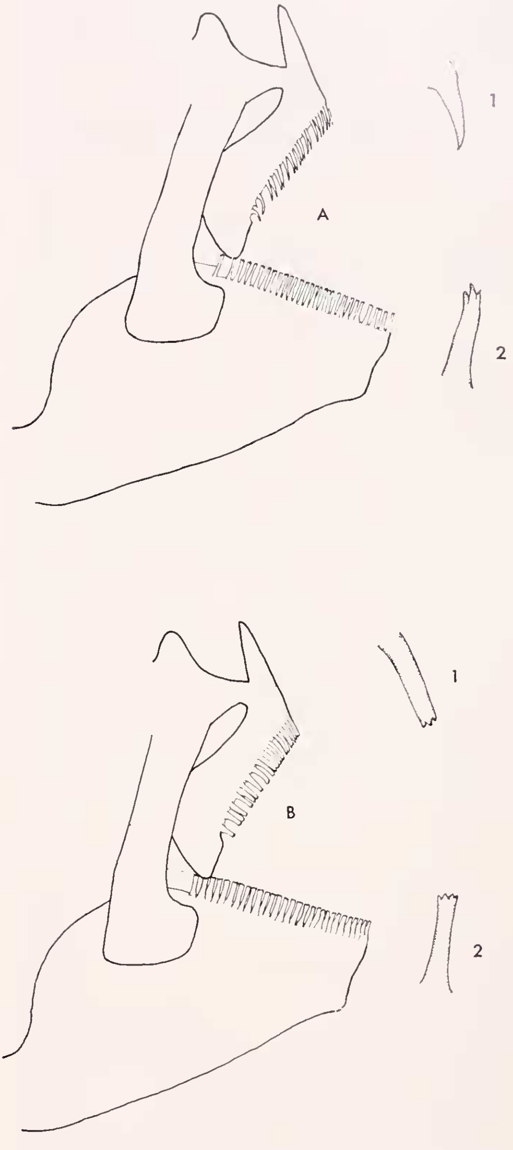


Figure 33. Jaws and teeth of two species of *Peprilus*: A = *P. paru*; B = *P. burti*; 1 = tooth of upper jaw; 2 = tooth of lower jaw. From cleared-and-stained specimens.

serial, and laterally compressed. The teeth of the upper jaw are slightly recurved, either simple and pointed (Fig. 33a), or have three small cusps (Fig. 33b). The teeth of the lower jaw are similar to those of the upper, but have either three cusps (Fig. 33a), or four or five cusps (Fig. 33b), and are not recurved.

The jaw apparatus seems suited for nipping parts from larger objects or for taking small objects whole. The significance of the differences in cusp pattern of the premaxillary teeth among the species of *Peprilus* is unknown. No teeth are present on the vomer, palatines, or basibranchials.

The gill rakers are long, slender, closely spaced, and beset with small teeth. They appear to serve as an effective screen in preventing small food particles from entering the gill area or from escaping through the opercular opening. However, they do not appear to serve as a straining device. Small differences in the number of gill rakers among the species of *Peprilus* do not seem sufficient to indicate differences in food habits.

The suborder Stromateoidei is characterized by toothed pharyngeal sacs located immediately behind the last gill arch. Bühler (1930) showed the sacs to be of pharyngeal origin and worked out the morphology of them in two stromateoid families, the Centrolophidae and the Stromateidae. Haedrich (1967) has studied in detail the comparative structure of the sacs in the five stromateoid families. The sac has muscular walls and appears to function as a shredding or grinding organ; and stomach contents are often shredded beyond recognition.

Immediately posterior to the pharyngeal sac is the short and thick-walled esophagus.

The stomach is a distinct, thick-walled, muscular, and roughly U-shaped organ which is capable of considerable distension.

The intestine is long, about two and one-half to three times the length of the body in *Peprilus*, and arranged into long loops in the body cavity. The intestine of fishes is generally considered to be the site of absorption. At the anterior end of the intestine is a dendritic mass of pyloric caeca. These structures, which develop as blind outgrowths of the anterior end of the intestine, are present in a number of families of teleost fishes. The number of caeca may vary greatly, from one to more than 1000 (Suyehiro, 1942). Suyehiro estimates there to be about 600 in the stromateid fish, *Pampus argenteus*. There are several hundred long, narrow caeca in *Peprilus*. It has been suggested (Al-Hussaini, 1947; Barrington, 1957) that the caeca are merely an adaptation which increases the surface area of the intestinal epithelium of fish in which the size of the body cavity limits the length of the intestine itself, or whose habits are carnivorous. Both of these criteria apply to *Peprilus*. The body cavity is small, probably because of other selection pressures for a short, compressed body. The fishes are also carnivorous, but there is no close correlation between gut length and food habits.

Food of *Peprilus* appears to consist of not only jellyfish but also small fishes, a variety of small crustaceans, and other small invertebrates. The pharyngeal sac is formed very early in life, at least by a size of 10 mm SL, and the young apparently feed in a manner similar to the adults. Juvenile *Peprilus* may eat proportionately more jellyfish than do the adults.

ASPECTS OF LIFE HISTORY AND ECOLOGY

Emphasis here is placed upon the four better known species, *P. triacanthus*, *P. burti*, *P. paru*, and *P. simillimus*. Little is known of the life history of the other three species. It seems reasonably certain that the overall biology of the latter species will prove not to be substantially different from that of the other species. The fishes of this genus are similar and wherever they occur fill a similar niche in the ecosystem.

Early life history. The testes, ovaries, and eggs are similar among all the species. Dioecy seems to be the rule in the genus. Eggs are buoyant, transparent, spherical, and contain one or more oil globules. Egg diameters range from 0.75 to 0.79 mm in *P. triacanthus*, and 70 per cent of the eggs have a single oil globule (Colton and Honey, 1963). They reported that other eggs had two or three smaller oil globules. Eggs of *P. paru* in Chesapeake Bay are approximately 1 mm in diameter (Hildebrand and Schroeder, 1927). Ovaries in a ripe fish occupy more than one-half of the body cavity. Maturity is reached in *P. triacanthus* at about two years of age (Bigelow and Schroeder, 1953), and at a length of about 140 to 180 mm SL; however, I have examined nearly ripe individuals which were as small as 120 mm SL. The size at maturity of the smaller species such as *P. burti* and *P. ovatus* is probably less than that for *P. triacanthus*. Hatching time for *P. triacanthus* is around 48 to 72 hours, and size of larvae at hatching is slightly less than 2 mm (Pearson, 1941; Colton and Honey, 1963).

The identification of larval *P. triacanthus* and *Urophycis chuss*, the squirrel hake, has been confused. Pearson (1941) and Miller and Marak (1959) indicate that the early larval stages considered by Kuntz and Radcliffe (1918) to be *P. triacanthus* are those of *Urophycis chuss*. Colton and Honey (1963) have shown that eggs of *P. triacanthus* differ from those of *U. chuss* described by Hildebrand and Cable (1934).

Spawning generally occurs in the spring and early summer, although the period of spawning may be longer in some of the warm-water species. Bigelow and Schroeder (1953) indicate that spawning of *P. triacanthus* in the Gulf of Maine begins in June, is at a maximum in July, and continues into August. Pearson (1941), on the basis of appearance of larvae, postulated a late spring and early summer spawning for *P. triacanthus* and *P. paru* in lower Chesapeake Bay. *P. paru* in the Gulf of Mexico apparently spawns in the spring (J. M. Miller, 1965). On the basis of the occurrence of young in winter and spring, Miller suggested a winter and possibly an autumn spawning for *P. burti.*

The type of eggs, the seasonal distribution of mature individuals, and the larval distribution should give some indication of the area of spawning. The eggs are buoyant and transparent which indicates that they are pelagic and near the surface. Kuntz and Radcliffe (1918), and Bigelow and Schroeder (1953), stated that spawning in *P. triacanthus* occurs a few miles offshore. Mature individuals are known to leave inshore waters during the spawning season, and those returning later are spent. Schaefer (1967) reported that *P. triacanthus* of spawning size does not appear in the surf zone until June, which indicates that before this time the fish were offshore. According to Miller (1965), *P. burti* moves offshore with increasing water temperatures in the spring, which indicates that spawning is offshore. Data from M/V GILL cruises along the coast of the southeastern United States show that *Peprilus* sp. larvae are several miles offshore. Larvae of *P. simillimus* occur both near shore and several miles offshore, but generally in large protected areas (Fig. 39). Offshore concentrations of both larvae and mature fish of this species suggest that spawning is generally a few miles offshore in surface waters.

Almost nothing is known of the spawning act. Aggregations of mature fish probably develop in offshore waters followed by mass extrusion of reproductive products. There is probably little courtship behavior before the spawning act. No external sexual dimorphism has been detected except the distension of the abdomen of ripe females. Segregation of males and females is not known to occur; large collections usually contain both sexes in reasonably equal numbers.

The eggs and early larval stages are in the surface layers and constitute part of the plankton. Ahlstrom (1959) stated that larvae of *P. simillimus* occurs between the surface and a depth of 48 m. Plankton volume data of the California Current Survey (Staff, South Pacific Fishery Investigations, 1956; Thrailkill, 1957, 1959, 1961, and 1963), in combination with information supplied by Dr. Ahlstrom, show that the larvae of *P. simillimus* are in the surface layers usually at depths of 50 m or less. Larvae which I identified as *Peprilus* sp. and which were taken on M/V GILL cruises off Georgia and South Carolina were in the surface layers to a depth of 72 m.

Distribution of larvae of *P. simillimus* on the Pacific coast (Fig. 39) is mostly near shore and in bays or other protected areas, although many were collected at considerable distances from shore. The greatest numbers of larvae are taken mainly around Cedros Island and Bahía Sebastián Vizcaíno off upper central Baja California, and smaller concentrations are taken in the Channel Island area near Los Angeles and near Bahía Magdalena off lower central Baja California (Figs. 39 and 40). Bigelow and Schroeder (1953) stated that although a considerable number of eggs of *P. triacanthus* are produced in the Gulf of Maine, very few larvae are taken there. They reported that no young *P. triacanthus* have been taken in the Bay of Fundy, but that they are very plentiful along the shores of southern New England. That juveniles of

Peprilus occur in bays and other inshore areas during the summer has also been shown by Reid (1955) for *P. paru* in Texas, Mansueti (1963) for *P. paru* and *P. triacanthus* in Chesapeake Bay, and by Schaefer (1967) for *P. triacanthus* in the surf zone of Long Island, New York.

In summary, the young of *Peprilus* appear to move inshore after hatching in pelagic surface waters to bays and other protected areas which serve as favorable nursery grounds. This general inshore movement coincides with the presence and abundance of certain coelenterates with which the young fishes of this genus associate in the summer and early fall (Mansueti, 1963).

Distribution in relation to certain physical factors.

Temperature. Temperature is probably the most significant factor affecting the distribution of members of the genus *Peprilus.*

Stromateids are basically warm-water fishes and secondarily have invaded temperate regions. *Stromateus* off southern South America and off southern Africa, and *Peprilus* in the western North Atlantic off Newfoundland and in the eastern North Pacific off British Columbia, represent the farthest penetrations into temperate waters.

Peprilus in its most northerly range is not abundant and generally is regarded as a summer visitor. Even though limited by temperature, some members of the genus do occur over a wide range of temperature. *P. triacanthus* off the northeastern United States is found where bottom temperatures range in autumn from 4.4° to 20.6°C (Fritz, 1965). Data from groundfish surveys (Figs. 34–36) off the northeastern United States show that *P. triacanthus* has been taken over areas where the mean bottom temperatures ranged from 5.0° to 14.2°C, these figures representing the total range for summer, autumn, and winter for the years 1963 to 1966. Schaefer (1967) has collected *P. triacanthus* in the surf zone of Long Island in August in water temperatures as high as 21.6°C. *P. burti,* a close relative of *P. triacanthus,* has been taken in waters of temperatures as high as 28°C and as low as 12.6°C (Gunter, 1945). *P. paru* has been collected in waters ranging in temperature from 13.7° to 30.0°C (Gunter, 1945) and from 14.6° to 27.5°C (J. M. Miller, 1965). *P. paru* is a shallow-water species, usually in waters of less than 50 m depth, and probably does not encounter as wide a range of temperatures as does *P. triacanthus. P. simillimus* on the Pacific coast probably encounters a range of temperatures similar to that of *P. triacanthus* since their latitudinal distributions are complementary.

The largely tropical and subtropical species of the Pacific, *P. medius, P. ovatus,* and *P. snyderi,* are almost certainly limited to a narrower, warmer range of temperatures than the above species.

Salinity. The habit of entering bays and even river mouths indicates that members of this genus are euryhaline. Reid (1955) collected a juvenile *P. paru* at a bayou mouth in a salinity of 10.3 ppm and two others at salinities of 17.3 and 17.6 ppm. Schultz (1962) collected *P. paru* in Texas bays in salinities ranging from 18.9 to 19.5 ppm. Gunter (1945) caught *P. paru* in the Gulf of Mexico in high salinities, 33.0 to 36.7 ppm. *P. burti* has also been collected in waters of widely varying salinity. Gunter (1945) reported that *P. burti* occurs in a salinity range of 15.6 to 35.2 ppm, but mainly in salinities over 30 ppm. Schultz (1962) gave a range of 21.5 to 25.9 ppm for *P. burti* in Texas bays. Schaefer (1967) recorded a salinity range of about 29.0 to 33.0 ppm for the surf waters of Long Island in which *P. triacanthus* is an abundant species. *P. burti* and *P. paru* have both been collected in Lake Pontchartrain, Louisiana (Tulane University Collections), a lake of varying salinity. *P. ovatus* has been taken at the mouth of the Colorado River (SIO 63–484) in the northern Gulf of California.

Currents. It is possible to correlate existing current patterns with the distribution of almost every species of *Peprilus*. The influences of currents in the distribution of the species of *Peprilus* is discussed below in the section on zoogeography.

Sediment or bottom type. In general, members of the genus *Peprilus* are distributed either over a sand or a mud bottom or a combination of both. None of the species are residents of rocky shores or coral zones, though they may occur in such an area temporarily. The preference for either a sand or a mud bottom is not usually species specific.

P. triacanthus off the coast of the northeastern United States is usually distributed over a sandy bottom or a combination of silt and sand. Fritz (1965) showed that the autumn distribution of this species is over the latter type. Bigelow and Schroeder (1953) stated that this species has such a decided preference for sandy bottoms rather than for rocky or muddy bottoms that few are taken in traps on muddy ground, while other traps along a sandy beach may yield considerable numbers. Leim and Scott (1966) report that small schools of *P. triacanthus* occur over sandy bottoms along the Canadian coast during the warmer months. In the southern part of the range of *P. triacanthus* there appear to be two distinct populations: one primarily in deep water and distributed over a mud bottom; and the other in shallow, inshore water over a sand bottom (Table 22). Most of the shelf area off the southeastern United States is sandy with some small areas of mud and gravel (Moore and Gorsline, 1960). While there seems to be a preference of each apparent population for either a sand or a mud bottom, there is overlap and no strict segregation. The apparent existence of two distinct populations in the Atlantic off the southeastern states is discussed on p. 247.

P. burti of the Gulf of Mexico is most frequently distributed over a mud or a sand-silt bottom (Table 22).

There are few data on the other species. *P. ovatus* in the northern Gulf of California has been collected over mud and sand bottoms. *P. simillimus* is found over both sand and mud bottoms.

Depth. Fishes of this genus may be found in waters as deep as 420 m on the continental slope (Table 22), but more frequently are found in much shallower waters.

Fritz (1965) reported that *P. triacanthus* occurs in a depth range of 30 to 270 m off the northeastern United States, but stated that the species is most abundant in 50 to 90 m of water. Data for other seasons (Figs. 34, 36, and 37) do not expand the above depth range.

Table 22 gives the depth ranges of *P. triacanthus*, *P. paru*, and *P. burti* off the southeastern United States and in the Gulf of Mexico. As mentioned earlier in the discussion of sediment type, *P. triacanthus* in its southern distribution has a wide depth distribution correlated with the possible existence of two separate populations or species in that region. This species has been taken in depths ranging from 20 to 420 m off the southeastern coast of the United States. The closely related *P. burti* in the Gulf of Mexico has a less extensive depth range with greatest abundance at a range of about 9 to 135 m. *P. paru* is a relatively shallow-water form which occurs in inshore areas throughout the year.

The depth distribution of *P. simillimus* is probably similar to that of *P. triacanthus*.

There is little information on the vertical distribution of the tropical Pacific species. *P. snyderi*, *P. medius*, and *P. ovatus* have been taken in inshore areas in depths of less than about 50 m. *P. ovatus* probably does not occur beyond this depth while *P. snyderi* may descend to greater depths. *P. medius* seems to compliment in the Pacific the ecology of *P. paru* in the Atlantic; thus, its depth range may be similar to that of the latter species.

Seasonal distribution and abundance. Seasonal movements are generally characteristic of the more temperate species of

TABLE 22. SUMMARY OF THE DEPTH OF CAPTURE AND ASSOCIATED MAJOR BOTTOM TYPE OF COLLECTIONS OF THREE SPECIES OF *PEPRILUS* MADE BY THE M/V OREGON AND M/V SILVER BAY IN THE SOUTHWESTERN NORTH ATLANTIC (CAPE HATTERAS TO SOUTHERN FLORIDA), AND IN THE GULF OF MEXICO FOR THE YEARS 1950 THROUGH 1966.

SPECIES	REGION	DEPTH RANGE (meters)	BOTTOM TYPE
P. paru	Atlantic	6–88	sand and/or mud
P. paru	Gulf of Mexico	2–115	sand and/or mud
P. burti	Gulf of Mexico	2–274	sand and/or mud; infrequently coral
P. triacanthus (deep-bodied)	Atlantic (generally inshore)	7–145	usually sand; less often gravel, mud, or mud and sand
P. triacanthus (shallow-bodied; often spotted)	Atlantic (generally further offshore)	20–420	usually mud; less often sand, coral, or mud and sand

the genus. Seasonal migrations apparently serve to maintain the species within a favorable range of environmental conditions.

The seasonal movements of *P. triacanthus* (the butterfish) have been generally recognized for some time. Bigelow and Schroeder (1953) indicated that while definite evidence is lacking, butterfish in the Gulf of Maine and southward seldom appeared to descend deeper than 25 to 55 m during the summer, and to spend the winter and early spring near bottom in depths down to about 180 to 210 m. Fritz (1965) showed that in the same area butterfish are in shallow, warm waters during autumn and are abundant at depths of 50 to 90 m and at a water temperature of 11°C. He suggested that the fish migrates northward into the Gulf of Maine during the summer months. Pearson (1932) reported that small quantities of butterfish have been trawled in offshore waters in winter in Virginia and North Carolina. Leim and Scott (1966) stated that small schools of butterfish occur over sandy bottoms along the Canadian coast during the period of warm water from May to November, but are offshore in depths to 100 fms (183 m) in the winter. Schaefer (1967) found that butterfish of a wide size-range occur in the surf zone of Long Island from June through October.

The distribution of *P. triacanthus* in summer, autumn, and winter over a three-year period in the Gulf of Maine and in coastal waters south to just beyond 40°N is presented in Figures 34 to 36. Length-frequency values of the total catch calculated from a sample length-frequency are given for each seasonal catch. Figure 37 shows the depth zones for the strata of this geographic region. The strata maps of Figures 34 through 37 were designed, described, and presented in extended form by Grosslein (1969).

P. triacanthus is widespread both in inshore waters and over deeper waters near the edge of the continental shelf in the summer months (Fig. 34). The fish occurs to a limited extent in the Gulf of Maine, especially in the southern portion. The greatest number of individuals were collected in strata nine and ten (Fig. 37), and in waters of less than 55 m in depth. The species was collected over an area in which the mean bottom temperatures ranged from 5.8° to 13.3°C and in waters ranging from 40 to 247 m in depth.

The autumn distribution (Fig. 35) is similar to that of the summer distribution.

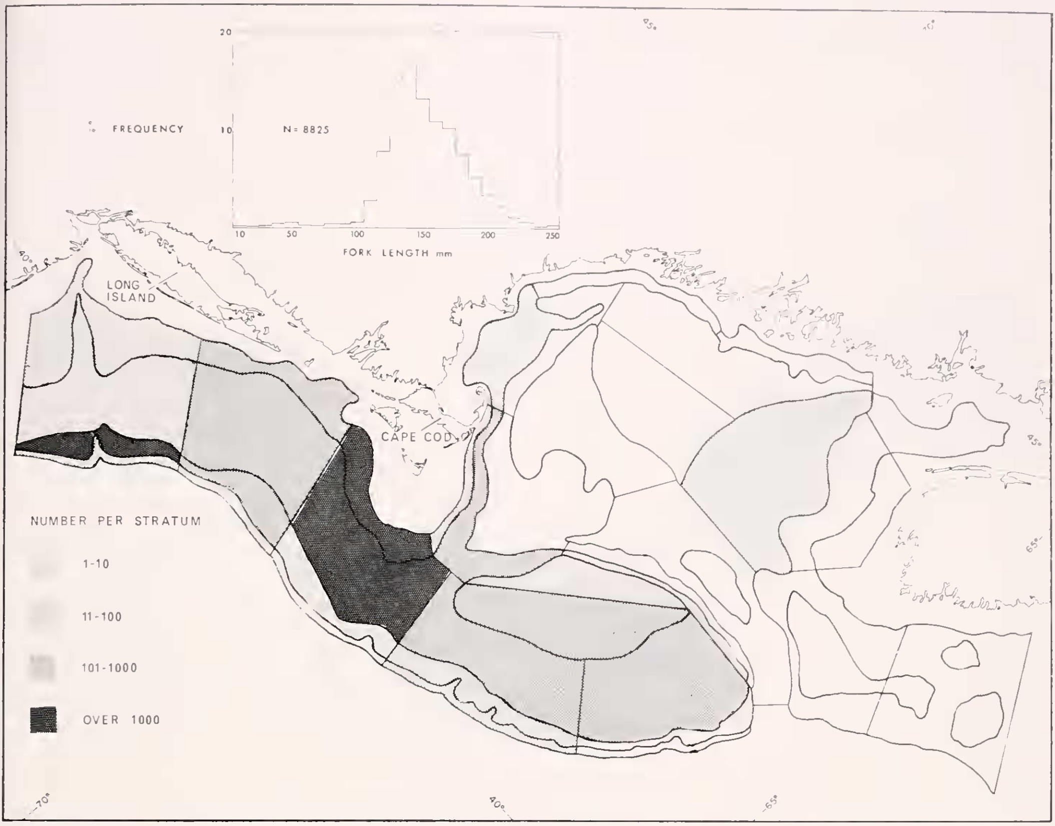


Figure 34. Summer (July and August) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1963–65. Data compiled from R/V ALBATROSS IV groundfish survey cruises of the U. S. Bureau of Commercial Fisheries, Woods Hole, Massachusetts. Number of fish per stratum is the cumulative total catch per stratum for the three-year period. Length-frequency is of the total catch calculated from the sample length-frequency; N = total catch of all strata for the three-year period. Strata map courtesy of Marvin D. Grosslein.

The greatest numbers of individuals were collected in stratum nine (Fig. 37), in waters of less than 110 m in depth. The species was collected over an area in which the mean bottom temperatures ranged from 5.8° to 14.2°C and in waters ranging from 33 to 250 m in depth.

The winter distribution (Fig. 36) is different from that of either the summer or the autumn. The winter collections made in the same region and with reasonably the same fishing effort, indicate that the species has a more restricted horizontal distribution during this season. The distribution is entirely south of the Gulf of Maine and in deep water. No fish were collected in the shallowest strata. The greatest numbers of individuals were captured in stratum seven (Fig. 37), in which the depth range is 112 to 183 m. Considerable numbers were collected in deeper water near the edge of the continental shelf. Collections were made over an area in which the mean bottom temperatures ranged from 5.0° to 10.2°C.

The spring distribution (no map, data for 1968 only) is similar to the winter distribution. The greatest numbers of individuals were collected in deep water along the edge of the continental shelf. The fish was

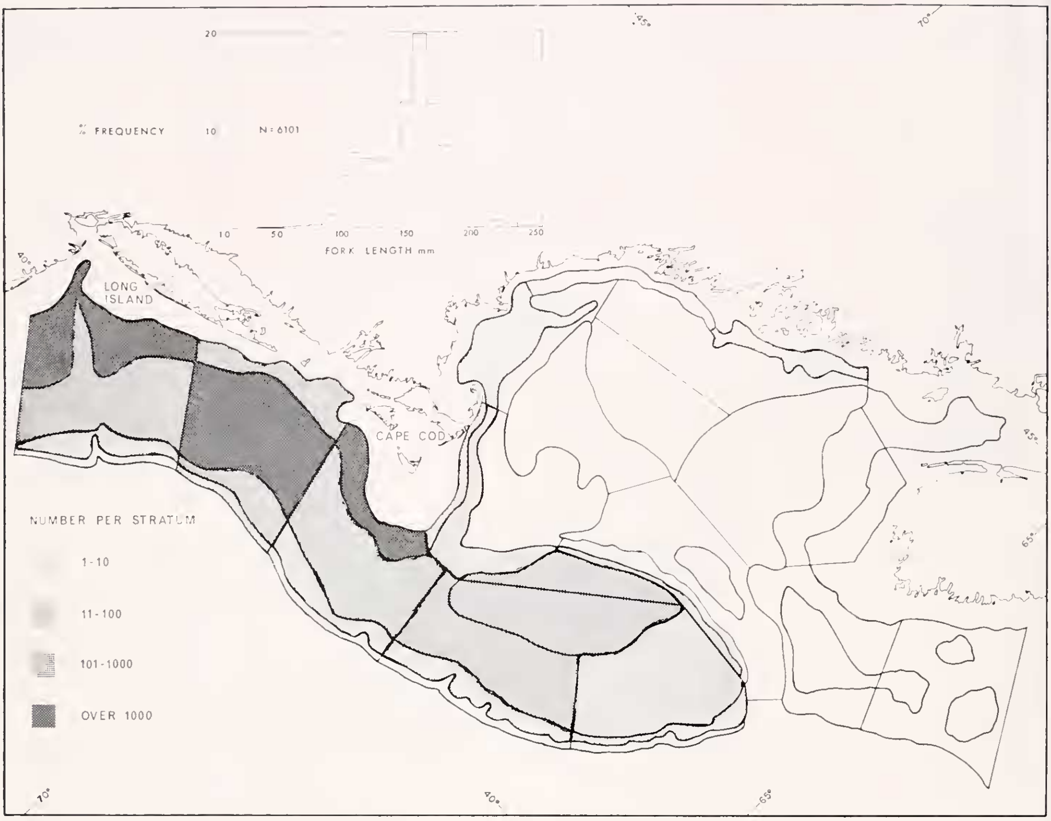


Figure 35. Autumn (October, November, and early December) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1963–65. Explanation of symbols and other information in Figure 34.

captured in waters ranging in depth from 44 to 274 m.

In the summer months along the coasts of the middle and northeastern Atlantic states, *P. tricanthus* has a wide, shallow-water distribution with movements both inshore and northward. The autumn distribution is similar. During the winter the species becomes restricted horizontally and concentrated in deep, offshore waters near the edge of the continental shelf. This winter concentration appears to be influenced strongly by water temperatures, and even though the seasonal distributions are different, the ranges of mean bottom temperatures strongly overlap for all seasons. The early spring distribution is similar to the winter distribution. In late spring, May to June, the species moves inshore and northward as upper level water temperatures begin to rise. The fish then assumes the summer distribution described above.

As spawning continues or is completed in late spring and summer, subadult and mature individuals of *P. triacanthus* range widely in shallow waters and occur in the surf zone from June through October on Long Island (Schaefer, 1967). Schaefer has shown that in June surf zone catches are mainly of large individuals, many of which are large enough to have already spawned offshore. In July, fish of a wider size-range are captured in the surf zone. The length-frequency diagram presented by Schaefer for August is bimodal with all

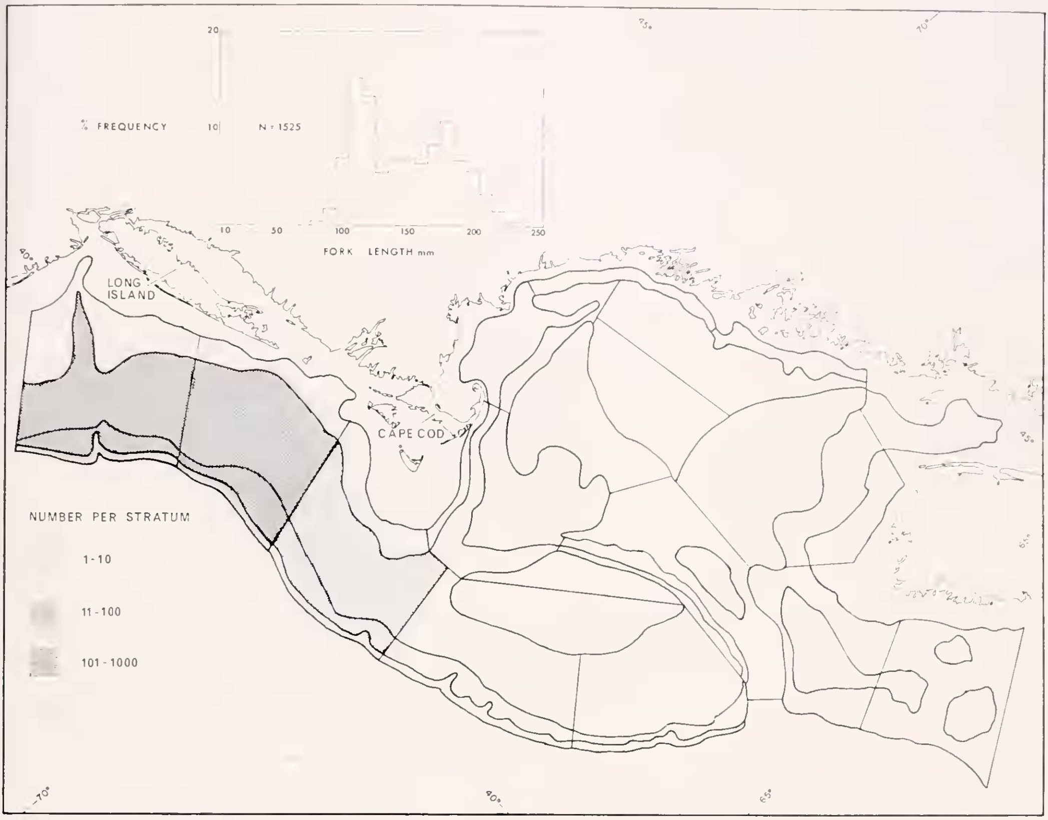


Figure 36. Winter (January and February) distribution of the butterfish, *Peprilus triacanthus*, off the northeastern coast of the United States, 1964–66. Explanation of symbols and other information in Figure 34.

fish of 100 mm FL (fork length in *P. triacanthus* approximately 10 per cent greater than SL) or less. This indicates that juveniles spawned earlier in the year are now entering the surf waters along with larger juveniles. Still larger fish were captured in August, September, or October. These large individuals probably move long distances during the summer and autumn even into waters as far north as Newfoundland and the Gulf of St. Lawrence.

The seasonal distributions and length-frequency diagrams (Figs. 34–36) do not include surf zone catches but only captures from trawlable waters. The length-frequency data seem to correlate well with Schaefer's (1967) data from the surf zone. In summer (Fig. 34), the diagram is essentially unimodal at around 140 mm FL, but it also indicates the presence of juveniles of 50 mm or less. All the fish were collected with a standard 36′ trawl having a one-half inch mesh codend liner; the use of a finer mesh probably would have resulted in the capture of more small fish. The data for autumn (Fig. 35) are weakly bimodal and consist mostly of large individuals of around 160 mm FL. This corresponds with the surf zone data which indicated that such large fish were absent from the surf in autumn. This further suggests that different size groups move independently, at least during the summer and autumn. The length-frequency diagram for winter (Fig. 36) is strongly bimodal with one peak around 100 mm,

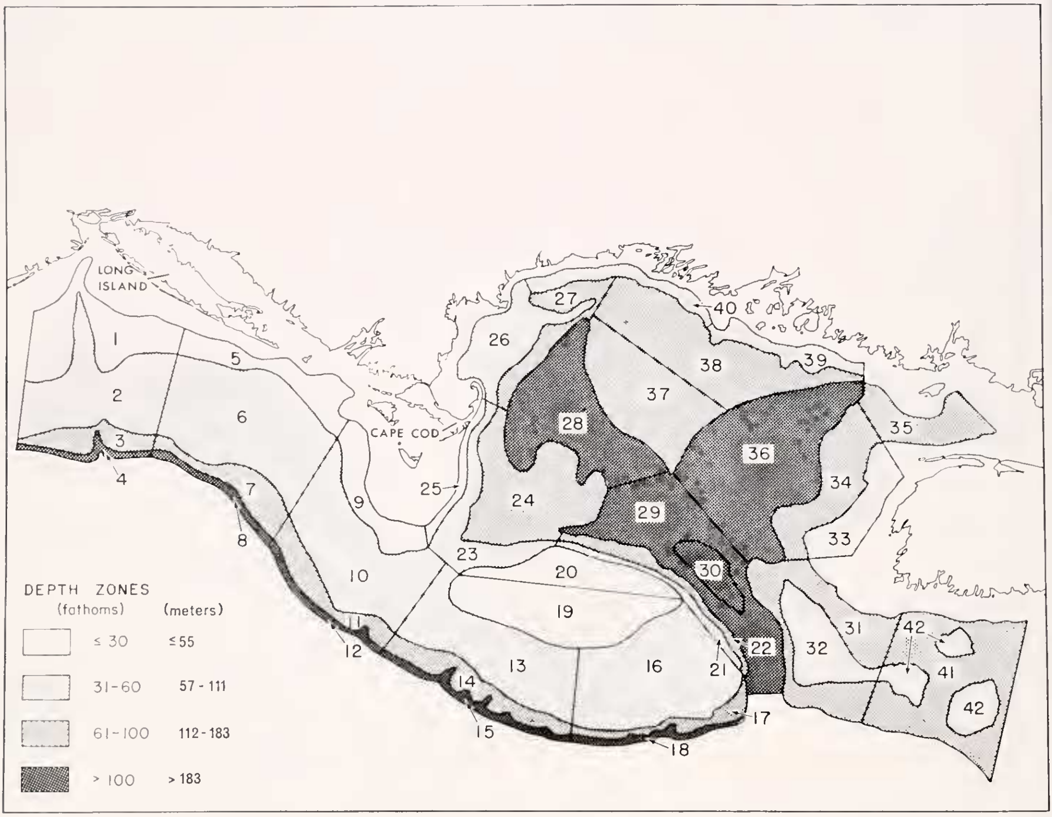


Figure 37. Strata map with depth zones corresponding to Figures 34 to 36.

another around 180 mm, and has a total size-range of 70 to 230 mm FL. The length-frequency diagram for the spring (Fig. 38) is similar to the one for winter. The curve is bimodal with one peak at around 100 mm and another at around 140 mm, but with many larger individuals. The total size-range is from 70 to 210 mm FL. These data for the winter and spring months indicate that two- and possibly three-year classes are concentrated in deep water during these seasons. Thus, there seem to be wide dispersal and independent movement of size-classes in the warmer months, and a concentration of a large part of the population in deep water in the colder months.

The seasonal distribution of *Stromateus maculatus* (=*Stromateus brasiliensis*) off the southern Atlantic coast of South America parallels in some respects that just described for *P. triacanthus* in the western North Atlantic. T. J. Hart (1946) described the main features of the seasonal movements of *S. maculatus* on the Patagonian shelf as follows: a double trend of seasonal movement – inshore in spring and summer with maximum concentration, offshore in autumn and winter with maximum dispersal; and, a meridional movement southward in summer and northward in winter. The latter aspect is similar to that of *P. triacanthus*, but, unlike the pattern of *S. maculatus*, maximum dispersal of *P. triacanthus* seems to occur in summer and autumn with maximum concentration in a restricted region occurring in the winter and early spring.

A number of fishes with warm-water af-

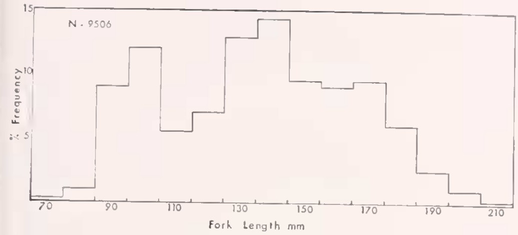


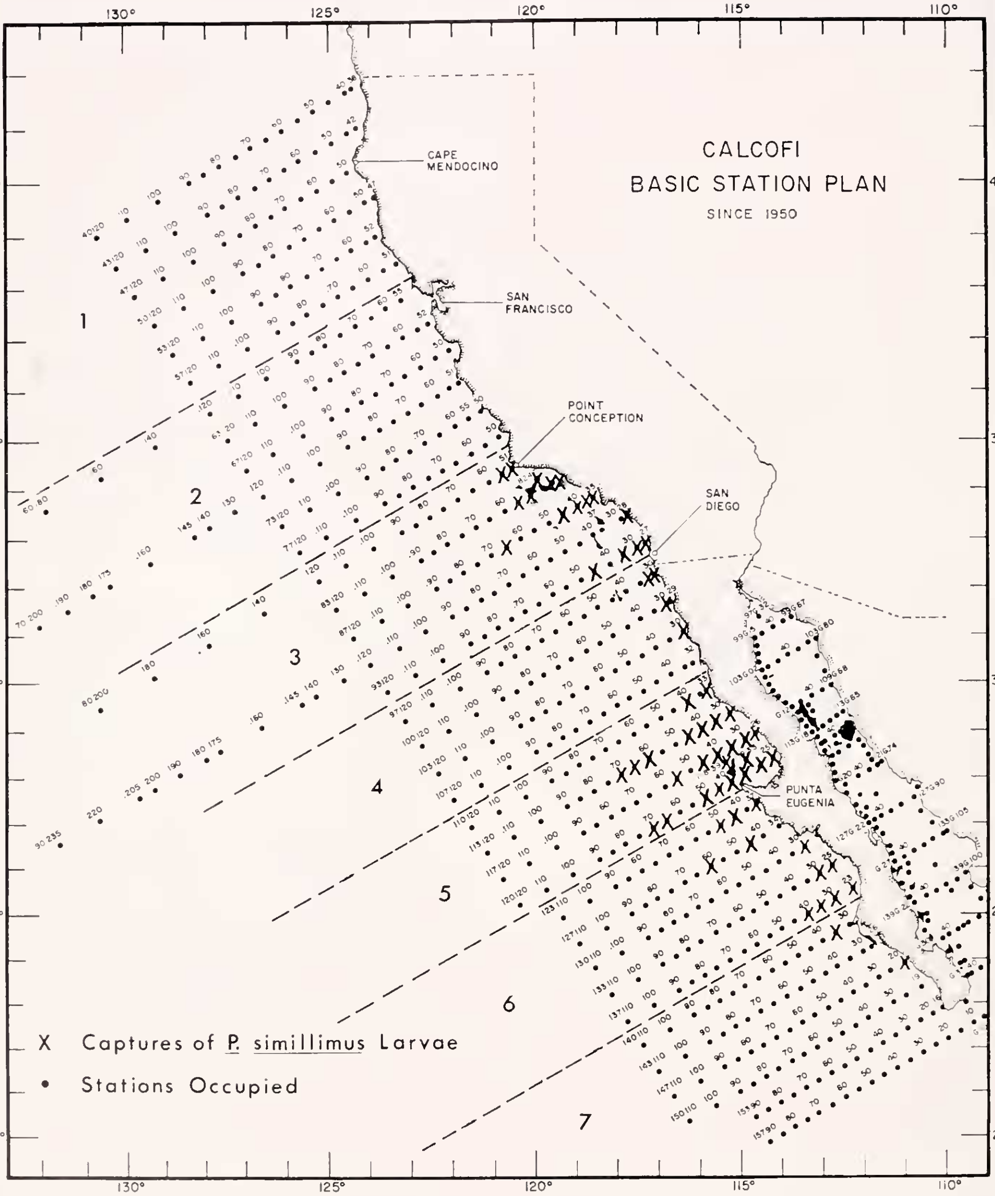
Figure 38. Length-frequency diagram for the spring (March, April, and early May) collection of butterfish, *Peprilus triacanthus*, made by R/V ALBATROSS IV groundfish survey cruises of the U. S. Bureau of Commercial Fisheries, Woods Hole, Massachusetts, off the northeastern coast of the United States, 1968. Length-frequency is of the total catch calculated from the sample length-frequency. See Figures 34 to 37.

finities migrate seasonally in a manner similar to *P. triacanthus.* Atlantic mackerel, *Scomber scombrus*, scup, *Stenotomus versicolor,* and weakfish, *Cynoscion regalis,* among others, migrate coastwards to their spawning grounds in spring and summer; before winter advances, when shallow, inshore waters become colder than those offshore, these species move offshore to warmer, deeper waters (Marshall, 1966). Whereas, cold-adapted fishes such as haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens,* may retreat in summer from warm, inshore waters to cooler, deeper reaches. Cape Cod is often recognized as the southern boundary of most boreal species and the northern boundary of many temperate species (Fritz, 1965). Some fishes are restricted to either north or south of Cape Cod while others range seasonally into the adjacent region. The distribution of *P. triacanthus* largely is south of Cape Cod except in the summer and autumn when it migrates northward into the Gulf of Maine. According to Fritz, Atlantic cod, *Gadus morhua*, a typical boreal species, may migrate as far south as Virginia during the winter months when temperature conditions are suitable. Silver hake, *Merluccius bilinearis*, and spiny dogfish, *Squalus acanthias,* for example, range widely both north and south of Cape Cod.

The other species of *Peprilus* which might be expected to migrate seasonally is *P. simillimus,* since it ranges into temperate waters as far north as the southern coast of British Columbia. Ulrey and Greeley (1928) reported that the fish is abundant in summer especially around Santa Cruz, California. Recent publications (J. L. Hart, 1949; Batts, 1960; High, 1966) have cited either the increased abundance or local occurrences of *P. simillimus* in Washington and British Columbia waters. Hart also pointed out that an increase in poundage of landings had occurred in the Monterey Bay area of California, whereas, previously, the major portion of the landings had occurred in southern California. Hart's list of occurrences of the species in British Columbia waters mostly includes records for the winter months of December, January, and February.

The distribution of *P. simillimus* larvae off the coasts of California and Baja California (Fig. 39) strongly suggests the warm-water affinities of the species. From 1955 to 1959, larvae of this fish have not been collected north of Point Conception, California, about 34°N. The greatest abundance of larvae was taken in the upper central Baja California area (Figs. 39 and 40), mainly around Bahía Sebastián Vizcaíno. Larvae were collected in greatest numbers in the months of May, June, and July (Fig. 41), although they were taken from January through August. There seems to be no significant time difference between the appearance of larvae in the northern (Point Conception) and in the southern (southern Baja California) parts of the distribution.

Berry and Perkins (1966), in a survey of the pelagic fishes of the California Current area from central California to central Baja California, reported that *P. simillimus* ranging in size from 12 to 165 mm SL occurred from Point Conception to the vicinity of Cedros Island near Bahía Sebastián Vizcaíno, Baja California. This distribution agrees closely with that of the larval distribution just described.



Figures 39. Distribution of larvae of *Peprilus simillimus* off the coasts of California and Baja California, 1955–59: 1 = northern California; 2 = central California; 3 = southern California; 4 = northern Baja California; 5 = upper central Baja California; 6 = lower central Baja California; 7 = southern Baja California. Data compiled from collections made by California Cooperative Oceanic Fisheries Investigations (CALCOFI). Map courtesy of Elbert H. Ahlstrom.

Part of the adult population may move northward long distances along the Pacific coast during favorable periods. As has been mentioned, there have been reports of an increase in the northern abundance, yet the occurrence is still of sufficient novelty that reports continue to be published of the fish's capture in such northern

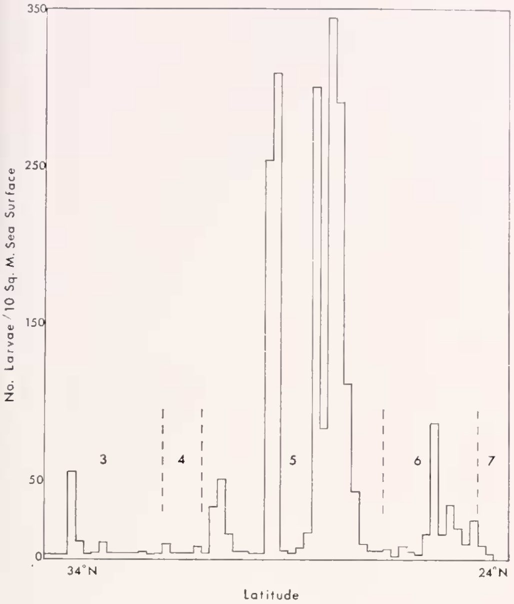


Figure 40. Relative regional abundance of larvae of *Peprilus simillimus* according to CALCOFI collections, 1955–59: 3 = southern California; 4 = northern Baja California; 5 = upper central Baja California; 6 = lower central Baja California; 7 = southern Baja California. The number of larvae per 10 square meters of sea surface is an estimate calculated from standard haul totals. See Figures 39 and 41.

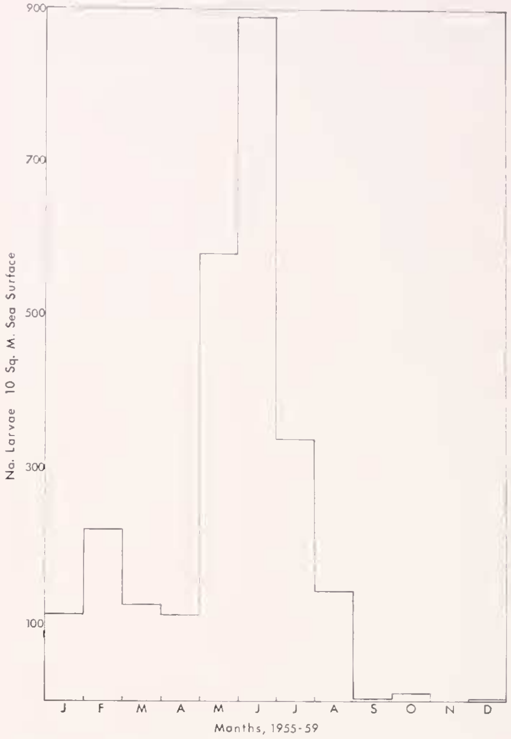


Figure 41. Cumulative monthly catch of larvae of *Peprilus simillimus* off the coasts of California and Baja California made by CALCOFI survey cruises, 1955–59. See Figures 39 and 40.

areas as Washington and British Columbia. The species remains to be of commercial importance only in California and mainly from Monterey to San Pedro.

Surface currents probably influence the extent of the northern distribution of *P. simillimus.* The data on the occurrence of this species in Washington and British Columbia are all similar in that the majority of captures are in the winter months, November through February, and that the size of the fish captured has been 150 mm FL or more. During the season of upwelling on the California coast (approximately March to July) a countercurrent (counter to the southward-flowing California Current) that contains considerable quantities of equatorial water flows close to the coast at depths below 200 m (Sverdrup, Johnson, and Fleming, 1942). In the fall upwelling ceases, and in the surface layers a countercurrent develops, the Davidson Current, which in November, December, and January flows northward along the coast to at least latitude 48°N. This latter current may particularly influence the movements of *P. simillimus.* Individuals may follow this current northward, and this may at least partially explain the captures of this species in northern areas in the winter months. In addition, the greatest numbers are landed commercially in California in the summer and fall with a decline in the catch in the winter and early spring (Fig. 43).

However, at least two factors cast some doubt on the proposal of a northward migration in winter and rather suggest the possibility of a resident, breeding population in the northern part of the range.

One factor is the gonadal condition of northern individuals. I have examined both male and female fish from Washington and British Columbia which had maturing and nearly mature gonads. These were fishes of 150 mm SL or larger. This is evidence for a northern spawning unless a southern migration occurs first. Eggs and larvae of this species have apparently not been found in northern waters.

A second factor which suggests a resident northern population is the apparent geographic variation which occurs in the length of the caudal fin. Individuals occurring from San Francisco to British Columbia have significantly shorter caudal fins than do those fishes taken from Monterey to Baja California (Fig. 14). Northern individuals also seem to have lower median fins than do southern forms. The importance of these variations is difficult to assess but it is suggestive of a distinct, resident population in the north, or at least of a clinal effect due to changing temperature conditions. The differences may only be between northern and southern California populations with those having the shorter caudal fin being resident off northern California and periodically migrating into more northerly waters.

While most northern occurrences have been in the winter months, *P. simillimus* has been collected at other times of the year. J. L. Hart (1949) reported that on 29 July 1946, about 150 pounds of this fish were taken in a bait seine in Bargain Harbor, British Columbia. Hart also quoted a crewman as saying that the species occurs throughout the year in British Columbia waters.

More information is needed in order to resolve the problems of breeding range versus geographic range and of seasonal migrations in *P. simillimus*.

P. paru, widely distributed in tropical, subtropical, and warm temperate waters in the Atlantic, is probably the most coastally-oriented fish of the genus. This species apparently does not migrate seasonally to offshore areas, but rather remains in relatively shallow water throughout the year (Table 22). H. H. Hildebrand (1954) caught *P. paru* during all months of the year on the shrimp grounds in the western Gulf of Mexico. Compton and Bradley (1963) reported that the fish was abundant in March at depths of 6 to 15 fms (11 to 27 m) in Texas coastal bays. J. M. Miller (1965) collected subadults in depths of 6 fms or less in the Gulf of Mexico near Port Aransas in February, March, and June. Copeland (1965) classed *P. paru* as a rare emigrant at Aransas Pass Inlet, Texas, and caught it in a tide trap in all seasons. I have collected mature and nearly mature individuals in the same tide trap during late June and early July. *P. paru* also appears to occur throughout the year in Chesapeake Bay on the Atlantic Coast.

P. burti occupies in the Gulf of Mexico a less extensive depth range than does *P. triacanthus* on the Atlantic Coast (Table 22). The species does, however, seasonally migrate to a limited extent.

Gunter (1945) collected *P. burti* in Aransas Bay, Texas, in March, August, and December; and in the Gulf of Mexico in March, April, May, June, and November. In Louisiana, the fish was taken most abundantly by Gunter in shallow areas in March. H. H. Hildebrand (1954) noted the presence of this fish on the shrimp grounds in the Gulf of Mexico throughout the year, but he stated that it was in greatest abundance in May and July, while during the winter it appeared sporadically and never in great abundance. Compton and Bradley (1963) found that it was one of the five most abundant fishes in Texas bay areas in March. They also stated that the fish breeds at a time of rising or high temperatures. According to J. M. Miller (1965), *P. burti* moves offshore with increasing water temperatures in the spring. Copeland (1965) listed this species as an occasional emigrant at Port Aransas Inlet, Texas, taking it in tide trap collections from November through May and most abundantly in April. The pattern seems to be that individuals are in shallow inlets and bays during the winter and early spring; then as the water temperature increases, the fish move offshore into the Gulf, yet not into much deeper water. Spawning probably occurs offshore in the surface layers of the Gulf during late spring, summer, and perhaps early fall.

The seasonal movements of *P. burti* seem to correlate with the temperate affinities of the species. The movements are the reverse of that of its close relative, *P. triacanthus*, but similar in that both remain in temperate waters. *P. burti* avoids subtropical temperatures, and *P. triacanthus* migrates to avoid boreal temperatures in the northern part of its range.

Little information is available on the other three species. *P. ovatus* is a shallow-water species of restricted distribution in the northern Gulf of California and probably does not migrate seasonally. The species has been collected at depths of 45 m or less. *P. medius* is often collected in shallow water, including bays and inlets and in depths of 90 m or less. This species probably migrates seasonally only to a limited extent. *P. snyderi* has been collected in inshore areas; however, its rareness in collections suggests that it may periodically inhabit deep water.

Faunal associations. At a size of about 10 to 30 mm SL, a portion at least of the populations of the species of *Peprilus* becomes associated with scyphomedusae and siphonophores (hereafter, both referred to as jellyfish medusae). This association may continue until the fish reach a size of 100 mm SL. The relationship is a widely recognized and well-documented one. Mansueti (1963) has reviewed the literature of the subject and has provided new data on the symbiotic behavior between *P. paru* and the jellyfish, *Chrysaora quinquecirrha*. The association is widespread among the stromateoid fishes according to Haedrich (1967). The relationship also occurs in the Carangidae, a pelagic family, in the Gadidae, Girellidae, and Centriscidae, all demersal families, and in the Zaproridae, an abyssal family (Mansueti, 1963).

The importance of the association in the life of these fishes is not well understood. The young fish may gain several advantages from the relationship including protection from predators, a source of food (the jellyfish itself), a concentration of food resulting from presence of small invertebrates among the tentacles and under the bell of the jellyfish, a means of dispersal, and possibly a means of reducing interspecific competition. Walford (1958) stated that jellyfish are among the most valuable animals in the sea in that they give shelter to the young of a number of species of fishes. He added that the small fish travel with their host in the plankton, feeding around it within a radius of a few feet, darting to safety beneath the umbrella when threatened by enemies. The fish continue this mode of life as long as it is advantageous to them, e.g., until they are ready to become independent. Walford suggests that this association may be an essential stage in the life cycle of some fishes.

At least in the stromateid fishes, and particularly in *Peprilus*, the association may not be obligatory. I have collected two species of *Peprilus*, *P. burti* and *P. paru*, which were not with jellyfish, as have others for *P. triacanthus* and *P. paru* (Bigelow and Schroeder, 1953; Mansueti, 1963). Mansueti classifies the association as a temporary ecological phenomenon resulting from a series of extrinsic chance factors in which jellyfishes are the passive hosts and fishes the active opportunists. *P. paru* begins a commensal association by consuming plankton and other organisms found on or near the hosts and then gradually becomes parasitic as it feeds on parts of the medusa. Finally, in autumn, as a large non-symbiont, it becomes predatory upon the medusae. Cargo and Schultz (1966) stated that schools of *P. paru* larger than 50 mm in length may destroy large numbers of scyphozoan medusae in minutes.

The fish itself is apparently rarely killed or eaten by the medusae. According to Mansueti (1963), the nature of the symbioses suggests that most associated fishes have some immunity to jellyfish toxin, and that either the immunity is gradually acquired through gradual adaptation, or that some or all fish symbionts may possess natural antibodies. A protective agent may be present in the mucous secreted by symbiotic fish which may either inhibit nematocyst discharge or counteract the toxin after stinging occurs. Species of *Peprilus* do secrete considerable amounts of mucous, and the extensive canal system may be involved in achieving immunity as suggested by Miner (1936).

The temporary association between *Peprilus* and jellyfish may be discontinued because of several factors: rapid growth of the fish and feeding independently from the jellyfish; the physical size attained by the fish; seasonal changes in hydrographic conditions – cold water temperatures in late autumn resulting in the death of certain jellyfish such as *Chrysaora* in Chesapeake Bay (Mansueti, 1963); or, similar to the first factor, a change in food habits of the fish, such as feeding in deeper waters.

The association does not involve the entire population of the fish species, which is to be expected since it is considered to be a fortuitous relationship. Stromateid fishes are known to be nonsymbiotic at the same size and in the same months as symbiotic stromateid fishes. The contacts between fish and jellyfish may be explained by the random search of the fishes for concentrations of food with such movement bringing the two organisms into close association. The coincidence of a period of pelagic existence among the young fish in the same area of a high incidence of pelagic jellyfishes seems important in developing the association.

The association is not species-specific, at least in *P. paru, P. triacanthus*, and *P. burti. P. paru* is known to consort with five jellyfish genera, *Chrysaora, Chiropsalmus, Cyanea, Aurelia*, and *Physalia* (a siphonophore). *P. triacanthus* has been found with *Chrysaora, Cyanea, Stomolophus*, and *Physalia. P. burti* in the Gulf of Mexico is known to associate with *Stomolophus meleagris* and *Aurelia* sp. Specimens of *P. simillimus* of about 30 to 50 mm in length have been found with *Pelagia* (SIO H52–221 and 60–409). This information suggests that the association is a loose one and gives additional support to the theory that the relationship is largely a fortuitous one and not geared to a species-specific, obligatory condition. The association is unique in the sense that the symbiont is not physically attached to the host (jellyfish) but is free in the immediate vicinity. This may account for the looseness of the relationship and increases the difficulty of attempting to categorize the association.

The young of many pelagic fishes gather under a variety of animate and inanimate floating objects at sea. The objects may be seaweed, large living animals, driftwood, or rafts of various origins. Gooding and Magnuson (1967) refer to the floating object in the pelagic environment as being a relatively rare "superstrate" in an environment notable for its horizontal homogeneity. This superstrate, they suggest, has some of the same ecological significance to certain pelagic fishes that a substrate has to inshore fishes. They cite shelter from predation as probably the most significant factor in the evolution of fish communities that gather beneath inanimate drifting material in the open ocean. The fish-jellyfish association seems to be different in that it persists where the inanimate relationship may terminate (Mansueti, 1963). The fish-jellyfish relationship, even though temporary itself, seems to be of a more sustaining nature in that the host provides shelter, protection, and food.

If precise categorization and a more

Table 23. List of the Ten Fish Species Seasonally Collected Most Regularly and Abundantly with the Butterfish, *Peprilus triacanthus*, by R/V ALBATROSS IV Groundfish Survey Cruises (U. S. Bureau of Commercial Fisheries, Woods Hole, Mass.) off the Northeastern Coast of the United States for the Years 1963 through 1966.

Species	Summer (Jul–Aug)	Autumn (Oct–Nov–Dec)	Winter (Jan–Feb)
Spiny dogfish (*Squalus acanthias*)*	×	×	×
Little skate (*Raja erinacea*)*	×	×	
Haddock (*Melanogrammus aeglefinus*)	×	×	
Silver hake (*Merluccius bilinearis*)*	×	×	×
Squirrel hake (*Urophycis chuss*)*	×	×	×
Alewife (*Alosa pseudoharengus*)	×		
Yellowtail flounder (*Limanda ferruginea*)	×	×	
Winter flounder (*Pseudopleuronectes americanus*)		×	
Fourspot flounder (*Paralichthys oblongus*)		×	×
Longhorn sculpin (*Myoxocephalus octodecimspinosus*)		×	

* Butterfish known to be a part of diet.

complete understanding of the fish-jellyfish association are to be achieved, underwater observations in the natural environment and further careful laboratory studies are necessary.

Table 23 is a list of the species of fishes which were collected in greatest abundance with *P. triacanthus* over a three-year period during three seasons, summer, autumn, winter, off the northeastern coast of the United States (Fig. 37) by groundfish surveys of the Bureau of Commercial Fisheries, Woods Hole, Massachusetts. A number of the species are large carnivores and feed on small fishes. Some of them are known to prey on *P. triacanthus*, and probably all the species listed in Table 23 occasionally feed on this species. The importance of *P. triacanthus* as a forage species becomes especially evident since it probably forms a substantial portion of the diet of such commercially valuable species as haddock, silver hake, and squirrel hake.

The season of the year that certain of the species listed in Table 23 occur or are collected most abundantly with *P. triacanthus* reflects the habits and temperature affinities of these species as compared with the same characteristics of *P. triacanthus.* The haddock (*Melanogrammus aeglefinus*) is a boreal species inhabiting cool waters, particularly north of Cape Cod (41°N) (Fritz, 1965). *P. triacanthus* occurs north of Cape Cod only in the summer and early autumn when temperatures are warmer; hence, the two species are collected together only in summer and autumn. Yellowtail (*Limanda ferruginea*) are also collected with *P. triacanthus* mainly in the summer and autumn. The former species is apparently confined to shoal waters (Bigelow and Schroeder, 1953) which *P. triacanthus* abandons during the winter for deeper water. The longhorn sculpin (*Myoxocephalus octodecimspinosus*) is a winter spawner, probably in shallow, coastal waters (Bigelow and Schroeder, 1953), which would explain its absence in areas of concentrations of *P. triacanthus* in the winter. The little skate (*Raja erinacea*) and the winter flounder (*Pseudopleuronectes americanus*) are bottom fishes with a depth range extending only to about 136 m (Bigelow and Schroeder, 1953), which would tend to explain why both species are taken with *P. triacanthus* only in the summer and autumn. Three species, silver hake (*Merluccius bilinearis*), squirrel hake (*Urophycis chuss*), and spiny dogfish (*Squalus acanthias*), range widely both north and south of Cape Cod at various depths (Fritz, 1965), and, accordingly, the three are captured in abundance in all three seasons with *P. triacanthus*.

General food habits. Stomach contents of the fishes of this genus are often very difficult to identify. The type of material making up a portion of the diet and the shredding action of the teeth of the pharyngeal sac frequently result in stomachs containing chunks of whitish or transparent, amorphous tissue. No attempt has been made to present a quantitative account of food habits of any species. Rather, a general summary is given of the results of examination of food items which I have made in three species of *Peprilus* and of reports in the literature of food studies in this genus and in the related genus *Pampus*.

The teeth, mouth size, and digestive tract are very similar among all the species of *Peprilus*. Food habits and feeding behavior are probably similar in all species of this genus. Differences which do exist may be quite subtle and might result from shifts in diet with age, from an increase in size associated with a shift in mode of life, from seasonal availability of certain food items, or from niche separation and character displacement in sympatric situations. The latter possibility deserves investigation.

The species of *Peprilus* consume a variety of food items. Bigelow and Schroeder (1953) stated that *P. triacanthus* in the Gulf of Maine feeds on small fish, squid, crustaceans such as shrimp and amphipods, annelid worms, and to a lesser extent, ctenophores. Haedrich (1967) reported that the shredded transparent tissues which predominated in the stomachs he examined were probably jellyfish, ctenophores, and salps. I have examined the stomach contents of freshly captured specimens of three species, *P. triacanthus*, *P. burti*, and *P. paru*. In one group of specimens of *P. triacanthus* ranging in size from 24 to 41 mm SL, the stomachs were generally full of chunks of whitish material which was identified as parts of jellyfish, especially the tentacles. Jellyfish remains constituted the bulk of the stomach contents of 20 specimens of *P. burti* ranging in size from 55 to 100 mm SL. Crustaceans including small amphipods, shrimp, and zoea larvae, and postlarval fish were also present in the stomachs of these fish. The stomachs of a few large (up to 150 mm SL) specimens of *P. paru* contained jellyfish remains and small crustaceans.

The association of young *Peprilus* with jellyfish medusae seems to be correlated with the feeding habits of the fish. That the young fish feed on their jellyfish hosts has been reported on several occasions (Miner, 1936; Mansueti, 1963; Cargo and Schultz, 1966; and others). Mansueti made monthly collections of symbiotic *P. paru* and found that the stomachs of these fish invariably contained masses of whitish, coagulated material which he identified as parts of scyphomedusae. A small amount of other food items, mainly small invertebrate remains, were also found in the stomachs of these fish which ranged in size from 21 to 80 mm TL. Stomachs of small, nonsymbiotic *P. paru* examined by Mansueti also contained masses of coagulated medusan tissue, some small invertebrates, and other material, largely unidentifiable. The young fish considered to be nonsymbiotic may actually be symbiotic except that they were away from the host when captured. The association is admittedly a loose one.

Although medusae are usually considered to be low in nutrients and high in water content per unit volume, young *Peprilus* seems certain to derive some nourishment from the protein structure of jellyfish. Mansueti (1963) found that in aquaria, *P. paru*, satiated and markedly distended from voracious feeding on *Chrysaora*, rapidly lost the distension suggesting the efficient utilization of jellyfish tissue and absorption of the liquid contents. Jellyfishes may be an important source of protein for young fishes during the critical early stages of growth in the summer and autumn.

Changes in the feeding and other behavioral patterns appear to occur in young

Peprilus by late autumn. Autumn seems to be the period when the symbiotic relationship dissolves, at least in Atlantic coastal waters, particularly around Chesapeake Bay. This separation may be followed by a short period of voracious feeding upon scyphomedusae and ctenophores (Dunnington and Mansueti, 1955; Cargo and Schultz, 1966). The end of the association often correlates with a loss in hosts, especially of *Chrysaora* which undergoes mass mortalities with a drop in water temperatures in late October and early November (Mansueti, 1963).

The pattern seems to consist of feeding largely upon jellyfish until a size of about 100 mm SL is reached. The association ends as the fish increase in size and hydrographic conditions change. This is followed by continued feeding upon jellyfish but to a lesser extent. The diet then consists of proportionately more crustaceans, worms, squid, and small fish.

Suyehiro (1942) reported that another stromateid fish, *Pampus argenteus*, feeds principally on jellyfish in Japanese waters, although his conclusion was based on limited data. Nath (1966) in a study of the fishes off the Travancore coast of India found that *Pampus argenteus* was a macroplankton feeder and that the variation in diet of the species depended largely upon the seasonal changes in abundance of crustaceans and polychaetes. From November through March amphipods and copepods are abundant, and during this period these crustaceans predominated in the stomachs of *Pampus argenteus*. In April, the diet consisted almost entirely of crustaceans. By June, the crustaceans declined and were replaced in the diet by polychaete worms until September. Nath did not find medusae in the stomachs of this species. Kuthalingam (1963) found results similar to those of Nath with the same species in the Bay of Bengal. He reported that young *Pampus argenteus* ate primarily copepods and other small crustaceans, while the adult fish are principally a variety of small crustaceans, as well as larger crustaceans, polychaetes, and small fish. Menon (1942) stated that larger specimens of *Pampus chinensis* off the Trivandrum coast of India feed on fishes, mainly anchovies, and younger ones on crustaceans and polychaetes.

The above data on *Pampus* indicates that the food and feeding habits of these fishes depend upon such factors as size and growth rate of the fish, seasonal and local abundance of food organisms, and the type and length of symbiotic relationships.

Commercial importance. Some of the species of all three genera of stromateid fishes are of commercial value. The fishes are oily and all species which are used commercially are said to be of delicate texture and fine flavor. *Pampus* is the most important genus commercially of the suborder Stromateoidei. Species of *Pampus* are important food fishes along the coasts of India, China, and Japan, being much in demand and bringing a high price in most areas. Species of *Stromateus* support only local fisheries along the coasts of west Africa, Chile, Argentina, and Uruguay. The potential fishery value of the species along the coasts of the latter two countries is probably much greater than generally suspected (T. J. Hart, 1946). Three species of *Peprilus*, *P. triacanthus*, *P. simillimus*, and *P. paru* are of considerable commercial value, although the catch of each species is subject to large yearly fluctuations, and none of the species forms a major part of the fishery in their respective regions. *P. triacanthus* forms the largest fishery among the fishes of the genus.

P. triacanthus, commonly known as the "butterfish" in fisheries literature, is mainly of importance along the coasts of the northeastern and middle Atlantic states. Its fishery has been discussed by Hildebrand and Schroeder (1927) for the Chesapeake Bay region and by Bigelow and Schroeder (1953) for the Gulf of Maine. This species is landed in recordable amounts from Maine to North Carolina,

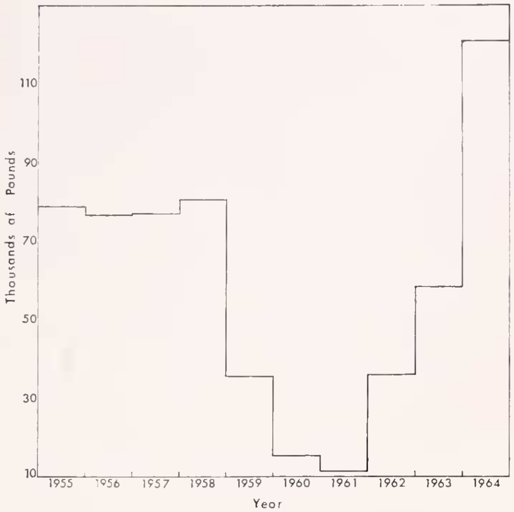


Figure 42. Yearly commercial catch of *Peprilus simillimus* off the coast of California, 1955–64. Data compiled from Staff, Marine Resources Operations (1958), Biostatistical Section, Marine Resources Operations (1960a, 1960b, 1961, 1963, 1964, 1965), and Greenhood and Mackett (1965).

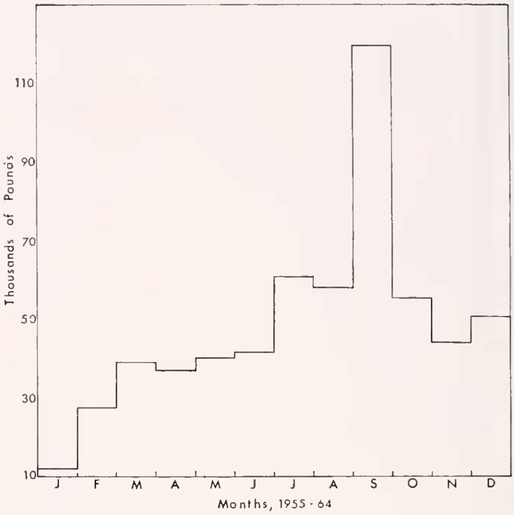


Figure 43. Cumulative monthly commercial catch of *Peprilus simillimus* off the coast of California, 1955–64. Source of data same as for Figure 42.

and the largest landings are in Rhode Island, New Jersey, New York, Massachusetts, and Virginia (Power, 1962; Lyles, 1966). The species is not of importance south of North Carolina even though its range extends to southern Florida. In Massachusetts, it is available in fresh fish markets throughout most of the year and is usually sold at a weight of about one-fifth to one-half pound and a length of six to nine inches. It is usually captured by otter trawl, haul seines, or pound nets. In the Chesapeake Bay region, about equal quantities are taken in the Bay proper and in oceanic areas. The characteristics of small body cavity, relatively soft bones, and high muscle content combined with its habit of forming large concentrations in winter in deep water may indicate that this species is of considerable potential value for use in the manufacture of protein supplements and fishmeal.

P. paru, the "harvestfish" of fisheries literature, is of important commercial value only on the Atlantic Coast of the United States despite its much wider distribution in the Atlantic. This species is landed in largest amounts in the Chesapeake Bay region mainly off Virginia and North Carolina. It was not recorded in the commercial catch either north of Virginia or south of North Carolina in 1960 and 1964 (Power, 1962; Lyles, 1966). *P. paru* is not sold in the Gulf of Mexico in any recordable numbers although it occurs throughout the region in considerable abundance. Baughman (1941) has stated that this fish does not reach sufficient size in Texas to be of economic value. The size difference seems to be slight, however. Small local fisheries may exist for this fish southward to Brazil. In the Chesapeake Bay region almost twice the poundage is landed in the Bay proper compared to the adjacent oceanic areas (Lyles, 1966). This demonstrates somewhat the inshore nature of this species compared to *P. triacanthus* which in the same region is caught in about equal amounts in the Bay proper and in oceanic areas.

P. simillimus, the "Pacific pompano" or just "pompano" of Pacific fisheries literature, has a wide distribution (British Columbia to southern Baja California), but is of commercial value only in the southern half of California from Monterey to San Diego. The biggest landings by far are in San Pedro and Monterey, California (Power, 1962; Lyles, 1966). The annual and monthly catches of this species fluctuate widely (Figs. 42 and 43) according to data compiled from Staff, Marine Resources Operations (1958), Biostatistical Section, Marine Resources Operations (1960a, 1960b, 1961, 1963, 1964, and 1965), and Greenhood and Mackett (1965). Largest monthly landings occur in the summer and early autumn. *P. simillimus* is a minor species in terms of the total catch; but with its rich flavor and flaky texture, it is considered a delicacy and brings a high price. It is sold entirely in fresh fish markets. The major portion of the catch is taken in lampara nets and purse seines, and a fair quantity is taken on hook-and-line by pier fishermen.

P. burti of the Gulf of Mexico apparently does not attain the size of its close relative, *P. triacanthus*, on the Atlantic Coast. As already mentioned, *P. paru* in the Gulf of Mexico is reported to not reach the size of members of populations of the same species on the Atlantic Coast. These two situations may illustrate the trend observed by Lindsey (1966) that fishes tend to be larger in higher latitudes. *P. burti* is of little or no commercial importance in the Gulf of Mexico. According to Gunter (1945), few members of this species reach large size in Texas waters and they are never sold for food there. H. H. Hildebrand (1954), who caught large numbers of this species on the Texas shrimp grounds, reported that the largest specimen caught measured 173 mm (SL or FL?). Gunter (1945) caught one specimen which measured 200 mm (SL or FL?) which may be nearly maximum size. *P. triacanthus* may reach a length of 300 mm FL.

No information is available on the economic status of *P. ovatus* in the northern Gulf of California, but, because of its apparently small size and restricted distribution, it is probably of little or no commercial importance.

The extent of the commercial value of *P. medius* and *P. snyderi* is uncertain although both species do appear in fish markets along the coasts of Mexico and Central America. Each species probably constitutes a minor element of the fishery in these regions.

EVOLUTIONARY RELATIONSHIPS AND ZOOGEOGRAPHY

A number of attributes of the stromateid fishes and of the genus *Peprilus* in particular invite study into the relationships and zoogeography of the group. The genus *Peprilus* is a member of an advanced family and has a widespread, continuous distribution along the coasts of the New World. Some of the species are widely distributed, two are more restricted, and all are confined to the continental shelf. None of the species cross oceanic barriers. *Peprilus* is largely allopatric with the other stromateid genera, and it is possible to correlate tectonic activity of recent epochs with the present distributional pattern of the members of the genus.

Origin of the genus Peprilus and its position among stromateoid fishes. Certain evidence suggests a Tethyan distribution for early members of the family Stromateidae or its ancestors. These fishes, though low in the number of species, were probably widely distributed in shallow coastal areas of the large Tethys Sea which in the early Tertiary combined the Indo-West Pacific, the Mediterranean, the tropical Atlantic, and the East Pacific faunas into one major unit (Ekman, 1953).

The first tectonic activity in the western Tethys which led to eventual isolation of the Mediterranean probably occurred in the early Tertiary (Fell, 1967). The disruption of the Tethys by emergence of land areas began in the Oligocene and was well developed in the Miocene (Kummel, 1961). From that time on the Indo-West Pacific realm was isolated from the western end of the Tethys Sea, and the Mediterranean Sea was formed.

The events described above may have divided and isolated segments of the ancestral stromateid fishes. *Pampus* probably evolved in isolation from other stromateids in the eastern Tethyan region. The ancestral stromateid stock in the western Tethyan region probably gave rise to *Stromateus* and *Peprilus*. *Stromateus* probably emerged in the Mediterranean and West African region, and in at least partial isolation, *Peprilus* probably evolved in the American region. The divergence of the evolutionary lines leading to *Stromateus* and *Peprilus* had possibly begun before the division of the Tethys Sea since Fell (1967) has indicated that passage and exchange of faunal elements through the western Tethyan region had become increasingly difficult before the Miocene.

Stromateus occurs along the southern coasts of South America and is the only stromateid to occur on both sides of an ocean. However, its transoceanic dispersal is across the shortest possible route, the South Atlantic. *Stromateus* of southern South America is similar to *Peprilus snyderi* of the eastern tropical Pacific. The two genera may share a common ancestor in the western end of the Tethyan element. *Stromateus* of South America has retained its generic affinities with *Stromateus* of Africa, but approaches *Peprilus* in several characteristics including: a reduced number of precaudal vertebrae; two epural elements in the caudal skeleton (three in the African *Stromateus*); and no pelvic fins in the young (see Haedrich, 1967: 102). Its systematic position seems to be somewhat intermediate between *Stromateus fiatola* of Africa and *Peprilus snyderi*. It may be more closely related to *Peprilus*, but further study is needed.

There was a direct connection between the Atlantic and Pacific Oceans before the formation of the Central American land bridge in the Pliocene, and there were probably few or no serious obstacles to widespread distributions of shallow, warm-water, marine organisms. The cooling of the climates which began in the middle and late Cenozoic and culminated in the Pleistocene glaciations (Kummel, 1961) apparently had not progressed by this time (lower Pliocene) so as to be a strongly limiting force to the distribution of tropical faunas. C. L. Hubbs (1960) has attributed in considerable part the low generic endemism in the Panamic fauna to the fact that this fauna is largely a part of the common Atlantic-Pacific tropical fauna of the New World. Hence, the stock of *Peprilus* was probably rather wide-ranging in an Atlantic-Pacific province of warm water. The distribution probably extended into what would be today temperate latitudes on the Atlantic and Pacific coasts. Few barriers existed to segregate populations, and speciation was probably at a low level.

North and South America became connected by an isthmus in the Pliocene (Schuchert, 1935; Lloyd, 1963; Simpson, 1950), and since that time, the Atlantic and Pacific faunas have evolved separately. The genus *Peprilus* has been divided geographically for several million years, depending upon the time of complete emergence of the isthmus and the duration of the Pliocene and the Pleistocene. After this separation, the cooling of the climates, the alternating effects of the Pleistocene glacial and interglacial periods, the resultant emergence and submergence of land barriers, and the establishment of persistent tropical-temperate conditions have provided the barriers for isolation and the resulting speciation in the genus.

Despite the basic morphological similarity among members of the genus, differences are apparent in body proportions, meristic values, premaxillary teeth, in the length of the anterior lobes of the median fins, and in the presence and size of body pores. Two somewhat subtle species groups, or at least two separate trends, exist within the genus. One group consists of relatively elongate fishes with low median fins; the species in this group are *P. snyderi*, *P. simillimus*, *P. triacanthus*, and *P. burti*. The second group exemplifies the trend toward a deep body and falcate median fins and is composed of *P. paru*, *P. medius*, and *P. ovatus*. Both trends or species groups apparently were established before the closing of the Central American seaway since each group is represented in both the Atlantic and Pacific oceans. Rosenblatt (1963) likewise has found that the two species groups of the tripterygiid genus *Enneanectes* are each represented in both oceans.

Primitive and derived conditions. Without fossil material, it is difficult and somewhat conjectural to attempt to determine which taxa within a group are primitive and which are derived. However, the situation becomes more approachable when a larger group containing the one in question can be placed in a reasonable evolutionary perspective. Haedrich (1967), largely on the basis of osteological evidence, has provided a concept of the evolutionary trends in the suborder Stromateoidei. Haedrich places the family Stromateidae at the zenith of stromateoid evolution and considers the ancestor of the family to be among the hard-spined members of the family Centrolophidae, probably a fish similar to the genus *Psenopsis*. Members of this genus are small (up to 200 mm SL), elongate, with small mouths, deciduous scales, the dorsal fin with only slightly more rays than the anal fin, and a vertebral number of 10+15.

I consider *P. snyderi* (Fig. 16) to be the most primitive species of *Peprilus* and most nearly like the ancestral form which gave rise to *Stromateus* and *Peprilus*, and probably *Pampus* as well. Compared to *Psenopsis*, all stromateids have an increased number of vertebrae and median fin-rays. *Pampus* and *Peprilus*, the latter especially, have lower meristic values than *Stromateus*, and Haedrich (1967) considers *Pampus* to be the most advanced stromateid genus. The ancestral or early stromateid forms probably had an increased number of vertebrae and median fin-rays relative to the centrolophid form from which they evolved. I therefore consider the high number of vertebrae and other meristics of *P. snyderi* to represent the primitive condition in the genus, and the reduced number to be the derived condition. *P. paru* (Fig. 24) is considered to be the most highly derived species, although no suggestion is made that this species is the most recently evolved. The divergence began early in the history of the group, before separation by the Central American land bridge, and has continued to the present. *P. paru*, with its very deep body and extremely falcate dorsal and anal fins, has diverged further from the presumed ancestral condition than any other member of the genus. *Pampus* has in several respects paralleled the evolutionary direction taken by *P. paru*.

A fairly strong continuum of types exists between the primitive type, *P. snyderi*, and the derived type, *P. paru*. This range of forms strongly supports the concept that this group of species constitutes a single genus rather than the three (including *Palometa* and *Poronotus*) in common usage. Although *P. paru* differs in several respects from *P. snyderi* and the other elongate species, its affinities with these species are strong. The group fits well into the category genus as defined by Mayr, Linsley, and Usinger (1953).

There does exist in *P. triacanthus* and *P. burti* the possible beginnings of another divergence or evolutionary direction. These two species have a row of relatively large pores of varying number and regularity below the dorsal fin (Figs. 19 and 21–22), and also have cusped rather than pointed or simple premaxillary teeth (Fig. 33b). The function of either attribute is unknown

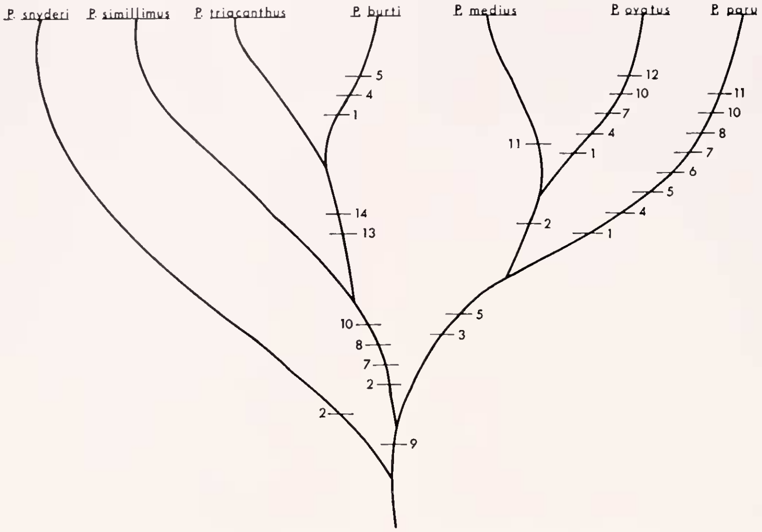


Figure 44. Dendrogram of probable species relationships in the genus *Peprilus*. The evolutionary steps which increase character-state codes for each character are shown as lines across the branches. The number of the character represented is next to the horizontal line and corresponds to one of the list of characters in Tables 24 and 25. Explanation in text.

and neither seems to represent as yet a major evolutionary shift. The presence of the row of pores has been used as a generic character; however, it does not appear to be specially innervated, but rather to be a slight elaboration of the subdermal canal system which is present in all the members of the genus. *P. ovatus* (Fig. 10) frequently has a series of medium-sized, irregularly-spaced pores along the dorsal surface of the body, a somewhat intermediate condition. Regarding the premaxillary teeth, two other members of the elongate species group, *P. snyderi* and *P. simillimus*, generally have pointed premaxillary teeth, but a particular specimen of either species may have a few teeth with two or three small cusps, an intermediate condition. In other aspects of morphology and ecology *P. triacanthus* and *P. burti* have strong affinities with the other members of the genus.

As Cain (1956) has stated, the genus is not necessarily definable by one peculiar attribute, nor are its constituents monotypic, equivalent, essentially merely subdivisions of it, or themselves wholly discrete. Inclusion of the seven stromateid species within a single genus appears to be a natural and instructive classification consistent with the evolutionary, morphological, and distributional characteristics of the members.

Intrageneric relationships. A dendrogram of species relationships in the genus *Peprilus* is presented in Figure 44. The dendrogram fits the definition given by Mayr, Linsley, and Usinger (1953) and the definition of a cladogram given by Camin and Sokal (1965). A time scale or a phylogeny is not inferred.

Several methods have recently been published (Edwards and Cavalli-Sforza, 1964; Camin and Sokal, 1965; Wilson, 1965) concerning the reconstruction of cladistic relationships based on the characters of contemporaneous species. In reconstructing the dendrogram of Figure 44, I have used the quantitative method of Camin and Sokal in association with con-

TABLE 24. CHARACTERS AND CHARACTER STATES APPLIED TO DENDROGRAM OF SPECIES RELATIONSHIPS IN *PEPRILUS*. Mean morphometric values in thousands of SL. See Table 25 and Figure 44.

CHARACTER	CHARACTER-STATE CODES 0	1	2
1. Eye diameter	x̄ 070–086	093–103	
2. Interorbital width	x̄ 087–097	112	
3. Pectoral fin length	x̄ 312–336	360–386	
4. Preanal distance	x̄ 424–445	465–484	
5. Body depth	x̄ 427–461	529–619	710
6. Caudal peduncle depth	x̄ 065–079	092	
7. Mean dorsal ray number	46.5–46.7	42.8–44.8	
8. Mean anal ray number	42.0–43.9	39.5–40.4	
9. Precaudal vertebrae	14–15	13	
10. Caudal vertebrae	20–22	16–19	
11. Anterior lobes of median fins	< 6 times length of shortest ray	≥ 6 times length of shortest ray	
12. Ratio of dorsal rays to anal rays	> 1.0	= 1.0	
13. Row of dorsal pores	absent	present	
14. Premaxillary teeth	simple	cusped	

ventional methods. The distribution of the species and the probable position of the genus in the suborder have been important in establishing the species relationships. The reasons for using the Camin-Sokal method are mainly for systematization and quantification and for increased objectivity. The method, although not greatly different from conventional methods, allows the procedure of reconstruction to be more easily followed.

The Camin-Sokal method requires several assumptions to be made: that characters be expressed in discrete states differing among at least some of the species; that characters can be arrayed in some logical order; that there is a knowledge of evolutionary trends so the characters can be arrayed in a presumed evolutionary sequence from primitive to derived; that the ancestral state arose only once in the taxa, although derived character states may have arisen repeatedly in different branches; and, that evolution is irreversible for each character state. The most parsimonious cladogram is considered to be the most plausible one. Primitive character states are coded as zero, derived states positively or negatively as required (Tables 24 and 25).

TABLE 25. DATA MATRIX OF CHARACTER-STATE CODES FOR THE SPECIES OF *PEPRILUS*. See Table 24 and Figure 44. Explanation in text.

CHARACTER	*snyderi*	*simillimus*	*triacanthus*	*burti*	*medius*	*ovatus*	*paru*
1. Eye diameter	0	0	0	1	0	1	1
2. Interorbital width	1	1	1	1	1	1	0
3. Pectoral fin length	0	0	0	0	1	1	1
4. Preanal distance	0	0	0	1	0	1	1
5. Body depth	0	0	0	1	1	1	2
6. Caudal peduncle depth	0	0	0	0	0	0	1
7. Mean dorsal ray number	0	1	1	1	0	1	1
8. Mean anal ray number	0	1	1	1	0	0	1
9. Precaudal vertebrae	0	1	1	1	1	1	1
10. Caudal vertebrae	0	1	1	1	0	1	1
11. Anterior lobes of median fins	0	0	0	0	1	0	1
12. Ratio of dorsal rays to anal rays	0	0	0	0	0	1	0
13. Row of dorsal pores	0	0	1	1	0	0	0
14. Premaxillary teeth	0	0	1	1	0	0	0

I began reconstruction of the cladogram using a total of 31 characters. Some of these could not be coded with any certainty or showed no differences among the species and thus provided no additional information. As a result, 14 characters were applied to the cladogram. These are presented in a data matrix with the appropriate character-state codes for each of the 14 characters (Table 25). The character states with the assigned character-state codes are listed in Table 24.

The primitive and derived character states were determined by examining the members of the genus in the perspective of the entire suborder. Certain character states correspond to apparent trends existing in the genus and represent conditions different from, or advanced relative to, the basal or primitive character states of some members of the genus or the presumed ancestral types of the suborder. The character states considered to be derived include: an increased eye diameter; a greater interorbital width; a longer pectoral fin; a greater preanal distance; increased body and caudal peduncle depths; and, lower numbers of dorsal and anal rays and of caudal and precaudal vertebrae (see Table 24 and the preceding discussion of primitive and derived conditions). The elongate lobes of the median fins, the approximate one-to-one ratio of dorsal and anal rays, the presence of a row of dorsal pores, and the cusped premaxillary teeth (characters 11, 12, 13, and 14; Table 24), are considered to be derived character states and were easier to code than the above states because they are discrete and unique to certain species in the sense of being present or absent.

The cladogram was reconstructed by the monothetic method described by Camin and Sokal. Evolutionary steps increasing character-state codes are shown graphically as short lines across the branches (Fig. 44). The number of the character represented by a short line is listed next to that line. It was necessary to test for parsimony and to make adjustments. The final cladogram requires 28 steps and is parsimonious in the context of information available.

The Camin-Sokal method was of use in determining the relationships of a newly described species, *P. ovatus*. The cladogram supports the assumption of a close relationship between *P. ovatus* and *P. medius*.

P. snyderi has the assumed primitive condition of all but one of the characters used in the reconstruction of the cladogram. The line leading to *P. simillimus, P. triacanthus,* and *P. burti* developed before the formation of the Central American land bridge. *P. burti* and *P. triacanthus* are seen as recently diverged species; *P. burti* has attained some advanced character states including a deeper body, a larger eye, and fewer vertebrae. The *paru-medius* line was probably divided by formation of the Central American land bridge. The high number of changes in character states for *P. paru* is illustrated in the cladogram and indicates the derived condition. *P. ovatus* secondarily approaches *P. paru* in a number of aspects including the short, deep body, the large eye, and the reduced number of vertebrae.

Parallelism and species pairs. As mentioned above, *P. triacanthus* of the Atlantic and *P. simillimus* of the Pacific closely resemble one another. Both are moderately elongate fishes with low dorsal and anal fins (Figs. 13 and 21). These two species show the closest similarity of any two in the genus in the summed differences of certain morphometric and meristic characters (Table 26). Their respective distributions complement one another on opposite coasts. Both reach their northern distributional limits at about 48°N, *P. triacanthus* as an occasional visitor on the southern coast of Newfoundland, and *P. simillimus* as an element in low abundance in coastal waters of southern British Columbia. The southern limits of their distributions are also similar. *P. triacanthus* ranges to about 27°N off the coast of southern Florida, with likely infrequent occurrences in the Gulf of Mexico; one record exists for the southeastern Gulf of Mexico (UW 13407). *P. simillimus* occurs as far south as about 24°30′N in Bahía Magdalena, Baja California; one specimen is known from the Gulf of California, in Bahía Los Angeles (SIO 62–236). Each species migrates seasonally in at least part of its geographic range.

P. triacanthus is of greatest abundance in the northern part of its range, North Carolina to the Gulf of Maine, as is attested by its relative abundance in the commercial landings in this region. *P. simillimus* is of most common occurrence in the southern part of its distribution, chiefly from San Francisco to Baja California. It is caught commercially only from Monterey to San Diego in California. Catches of the species in Washington and British Columbia are small and sporadic. The major surface currents, the Gulf Stream in the Atlantic, and the California Current in the Pacific, probably influence the regional distributions of *P. triacanthus* and *P. simillimus*, respectively.

P. medius in the Pacific and *P. paru* in the Atlantic seem to parallel one another morphologically and ecologically. Both species are deep-bodied with falcate dorsal and anal fins, but *P. paru* has diverged more sharply to become a very deep-bodied fish with extremely falcate dorsal and anal fins. Although little is known of the habits of *P. medius*, the available evidence suggests that both are essentially shallow-water species that do not migrate seasonally. The geographic ranges are complementary. *P. medius* is distributed from the southern Gulf of California to about 5°S near Paita, Peru, in the eastern tropical-subtropical Pacific and is largely confined within the limits of the 20°C surface isotherms. *P. paru* ranges from just north of Chesapeake Bay to throughout the Gulf of Mexico and the Caribbean region to southern Brazil and also has a tropical-subtropical distribution chiefly within the limits of the 20°C surface isotherms. The opposite pattern of surface currents in the Pacific relative to that in the Atlantic accounts for the disparity in the extent of the tropical-subtropical regions of the two coasts and apparently in the distributions of the two species. Whereas *P. triacanthus* and *P. simillimus* probably acquired temperate adaptations early in the Pleistocene, *P. paru* and *P. medius* seem to have had a continuous warm-water existence. *P. paru* has probably extended its range northward and southward into more temperate waters only since the last glacial period. The species has a continuous distribution around Florida which is indicative of warm-water affinities.

It is possible to postulate two possible mechanisms for the derivation of *P. ovatus*, apparently restricted to the northern Gulf of California. One mechanism is to consider it to have differentiated from *P. simillimus* stock off the outer coast of California and Baja California. C. L. Hubbs (1960) stated that during glacial periods the outer coast fauna was displaced southward to yield Pleistocene relicts in the upper Gulf of California. Walker (1960) counted 22 fish species endemic to the upper Gulf and added that a striking element of the upper Gulf fauna is composed of fishes common to the outer Baja California and southern California coasts, but absent in the extreme southern Gulf. In most cases the degree of differentation is slight. Walker is hesitant to suggest how the northern faunal element reached its present position. He offered the possibility that there may have been a movement through an oceanic connection which existed in the region of the La Paz plain during the late Pleistocene. If movement did occur through such a passage, only a slight general cooling of the waters of the Gulf would have been necessary to allow the entrance of cold-water forms from the outer coast. Because of a temperature front which exists in the cape region, a much more extensive cooling would seem to be required to allow movement around the cape of Baja California according to Walker.

However, *P. ovatus* is closer to *P. medius* morphologically, and I consider the former species to have been derived from *P. medius* stock even though the mechanism may be less obvious. Derivation from *P. simillimus* would involve an increase in the number of anal rays, in the number of caudal vertebrae, and an increase in body depth, eye size, and depth of caudal peduncle. Derivation from *P. medius* requires a decrease in the number of dorsal rays, in the number of caudal vertebrae, along with an increase in body depth and a decrease in the length of the anterior lobes of the dorsal and anal fins. The latter seems to be a more reasonable and coordinated change of character states and consistent with trends occurring in the genus.

Much of the upper Gulf is quite shallow with wide areas of shelf; the sediment is mostly sand with transition to mud in the delta area of the Colorado River (Walker, 1960). This type of habitat seems suitable for members of this genus, particularly ones closely related to *P. medius*, which seems to be a shallow-water species. Several factors may interact to prevent the southward movement of *P. ovatus* or the northward dispersal of *P. medius* into the upper Gulf: almost the entire Gulf coast of Baja California south of the area mentioned above is rocky, and few stromateid fishes have been collected along this coast; the shelf is narrow in the central Gulf region; temperature and salinity fronts exist in the southern Gulf; two islands with rocky shores are present in the central Gulf with a considerable extent of deep water south of them; increased wind convection and the more extreme ranges of sea surface-temperatures occur in the upper Gulf (Roden, 1958); and, a region of cold water exists around Isla Angel de la Guarda and adjacent islands in the upper central Gulf (Walker, 1960).

P. triacanthus and *P. burti* are the most closely related species in the genus. Their similarity has resulted in different taxonomic interpretations (Caldwell, 1961; Collette, 1963). *P. burti* occupies the now zoogeographically familiar "temperate pocket" of the Gulf of Mexico which in past epochs was continuous with the Atlantic Ocean of the United States because of the submergence of peninsular Florida. Both species are absent as residents from the southern part of Florida, the populations of both forming a disjunct distribution.

C. L. Hubbs (1960) considers the Gulf of Mexico to be geographically and zoogeographically analogous to the Gulf of California in that both contain Pleistocene relicts. Peninsular Florida has been variously submergent and emergent since the Miocene (Cooke, 1945). During the glacial periods of the Pleistocene when the sea level receded, Florida was a peninsula, and conversely, during the high stand of the sea of interglacial periods Florida was in large parts submerged (MacNeil, 1950). Thus, there have been opportunities for junction and disjunction of closely related populations. According to Hedgpeth (1953), the occurrence of nontropical species on both sides of Florida, but not in the southern part of the peninsula, apparently was as characteristic of Pleistocene periods when Florida was a peninsula as it is today. Hedgpeth characterized the Gulf of Mexico as a transitional zone between tropical and temperate regions with environmental conditions favoring invasions from one region or the other at some time during the year. Isothermal configurations presented by Hedgpeth, and studies on the coastal faunas of Florida, show that the southern part of Florida is more tropical than the upper regions. According to Briggs (1958), the shorefish fauna of Florida, particularly the southern element, has much in common with the fauna of the West Indies, South America, and Bermuda.

The degree of differentiation varies among species which have disjunct populations in the Atlantic and in the Gulf of Mexico. Some have diverged to the species level, others only slightly, and in most cases the decision as to rank is largely arbitrary. The situation has been described for certain species or has been discussed by several authors including Ginsburg (1952), Briggs (1958), R. J. Miller (1959), Caldwell (1961), Collette (1963), and Gutherz (1966) for fishes, and by Hedgpeth (1953) for crabs and molluscs.

The *burti-triacanthus* situation is complex and requires special mention. Caldwell (1961) considered the Atlantic and Gulf populations to be a single polymorphic species, *P. triacanthus*. He recognized three distinct populations of the species: 1) a deep-bodied form in the Gulf of Mexico (equivalent to *P. burti*); 2) a shallow-bodied form in coastal waters of the Atlantic north of Cape Hatteras and in waters usually deeper than 22 m to the south of Cape Hatteras; and 3) a somewhat intermediate form in shallow water of usually less than 22 m in depth south of Cape Hatteras. The Gulf population and the widely-distributed Atlantic population (2 above) are very closely related, but I have found the two forms to be distinct and, in combination with evidence given below, have reinstated *P. burti* as a valid species in the Gulf of Mexico. The morphological differences are in: caudal vertebrae number (17 in *P. burti*, 18–19 in *P. triacanthus*); body depth (Fig. 2); eye diameter (Fig. 3); and, the apparent lack of spots on the body in *P. burti* (Fig. 19) which are frequently present in *P. triacanthus* (Figs. 21 and 22). *P. burti* does not reach the size of *P. triacanthus*, occupies a less extensive depth range than *P. triacanthus* (Table 22), and appears to be less migratory between inshore and offshore waters than *P. triacanthus*.

A main problem is to explain the existence of the shallow-water population in the Atlantic (3 above), which presumably results in two distinct populations of the same species in the Atlantic south of Cape Hatteras. Caldwell (1961) gave two reasons for recognizing two such populations: 1) Mature individuals have been taken from both populations, and there is thus apparently no significant spawning migration; and 2) collections during each season of the year and in almost every month have produced specimens larger than 100 mm SL from most depths. In addition, I have found that most of the deep-water specimens in the Atlantic have been taken largely over a mud or silt bottom in waters up to 420 m depth, while the shallow-water form has been mainly collected over a sand bottom and nearer the coast (Table 22). The shallow-water form is deeper-bodied, usually has 17 or 18 (sometimes 19) caudal vertebrae, apparently has no spots on the body, and agrees closely with the description of *P. burti* (Fig. 19). The deep-water form (Fig. 22) is even more shallow-bodied than more northern members of *P. triacanthus* (Fig. 21), usually has 19 (sometimes 18) caudal vertebrae, and frequently has numerous spots on the body. There is likely some interbreeding between the two populations as evidenced by the overlap in vertebral number; however, the interbreeding is apparently not of the level that would result in the merging of the populations. No external sexual dimorphism or unusual sex ratios have been found in either population.

While it may be possible to explain the development and maintenance of two distinct populations in the same region by considering some type of hybridization, by presuming a strict segregation or divergence as to bottom type, or perhaps by assuming differential growth rates, I tend to favor as an explanatory device the speciation phenomenon of character displacement with the shallow-water population in the Atlantic being a disjunct element of the Gulf of Mexico species, *P. burti.*

Character displacement may be defined (Brown and Wilson, 1956) as the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened outside this zone. The characters involved may be morphological, ecological, behavioral, or physiological, the situation probably resulting most commonly from the first post-isolation contact of two newly evolved cognate species. Upon meeting, the two populations interact through genetic reinforcement of species barriers, or ecological displacement, or both, in such a way as to diverge further from one another where they occur together. Plasticity of the particular species may result in short-term ecological differences, say in food habits, in situations where species may infrequently come into contact. Whereas, character displacement should be considered as developing over a relatively longer period of time and involving genetic segregation as to morphology, ecology, and other characteristics.

Invoking character displacement requires that the probable history and vagility of the two species be considered. From a knowledge of the history of the genus discussed previously, it seems probable that the Atlantic and Gulf populations have existed since the beginning of the Pleistocene. *P. burti* and *P. triacanthus* or their precursor populations were probably continuously distributed and panmictic during an early interglacial period. A succeeding glacial period would have divided the populations and allowed differentiation and presumably isolating mechanisms to develop. Either during a following interglacial period when contact would have been facilitated, or because of an increased ability to migrate around Florida at some time in the recent past, members of *P. burti* have become distributed in shallow water in sufficient numbers to establish a breeding population in the Atlantic; and, in a first post-isolation contact have morphologically and ecologically displaced the southern members of *P. triacanthus* to the extent that the latter are further offshore, in deeper water, and largely over a mud-silt substrate. Kohn and Orians (1962) have stated that all cases of character displacement should involve displacement of ecological characters since the two species tend to exploit different niches where they occur together.

That these fishes have migrated or can migrate around peninsular Florida or at least are present on both sides of Florida is indicated by at least two pieces of evidence: 1) one record of a fish agreeing in all characters with *P. triacanthus* (especially the southern deep-water form) is known from the southeastern Gulf of Mexico, northeast of the Dry Tortugas (UW 13407); and 2) as has been described, individuals which agree quite closely to the description of *P. burti* have been taken in the Atlantic off Florida (USNM 156149, for example).

It is indeed difficult to advocate character displacement as occurring in the marine environment, especially since so many factors of the interaction cannot be observed or monitored. Although the above explanation is as yet only an hypothesis, the phenomenon of character displacement seems with present evidence to be a reasonable mechanism for explaining the existence of two distinct populations in a given region.

Faunal regions. Much has been written on the extent and delineation of faunal provinces of coastal marine organisms. Often the regions are expanded or contracted to suit the discussion of a particular group of organisms and to allow the greatest number of generalizations. Certain of the faunal boundaries, including ichthyological ones, remain speculative. In the discussion below, no attempt is made to alter the size of the provinces since the imprecise distributional knowledge of the species does not allow it.

Atlantic Coast. P. paru is distributed throughout the tropical-subtropical region of the western Atlantic and occupies a number of faunal subregions. In ranging from just north of Chesapeake Bay southward throughout the Gulf of Mexico and the Caribbean to southern Brazil, this species is largely confined within the limits of the 20°C surface isotherms (Sverdrup, Johnson, and Fleming, 1942), a boundary often cited for warm-water species. Warm currents flowing away from the equatorial regions result in a relatively wide expanse of tropical and subtropical conditions in the western Atlantic.

The southern limit of *P. paru* seems to concur with the faunal boundary and transition zone which begins at about 23°S in the region of Cabo Frio, Brazil. The partial boundary and transitional area are apparently created by the mixing of the waters of the cold, northward-flowing Falkland Current with those of the warm, southward-flowing Brazil Current, and have been discussed by several South American workers (Balech, 1954; Lopez, 1963; Stuardo, 1964; Vannucci, 1964). *P. paru* ranges southward as far as Buenos Aires, but is less common south of Rio de Janeiro in an area which is largely transitional between the tropical and south temperate regions (Balech, 1954).

P. paru, in the northern part of its range, occupies a somewhat transitional region between subtropical and warm temperate zones.

P. burti and *P. triacanthus* are fishes of more temperate waters than *P. paru. P. triacanthus* ranges from the Gulf of Maine to just south of Cape Kennedy, Florida, and thus occupies the so-called Transatlantic Province (Hedgpeth, 1953) which some authors divide into the Virginian, Cape Cod to Cape Hatteras, and the Carolinian, Cape Hatteras to southern Florida. The latter subregion is often considered to be a transitional or mixed zone. Cape Cod is often listed as the southern boundary of the Boreal Province but as Ekman (1953) has indicated, the fluctuating seasonal conditions of temperature in this area make it difficult to define a sharp boundary at Cape Cod. *P. triacanthus* is found seasonally north or south of Cape Cod. This illustrates that water conditions must be of primary importance in zoogeography rather than mere coastal configurations.

P. burti, found throughout the Gulf of Mexico, is a disjunct warm temperate element closely related to *P. triacanthus. P. burti* occupies the so-called "temperate pocket" of the Gulf of Mexico.

Pacific Coast. Until recently, two species of *Peprilus, P. snyderi* and *P. medius,* were known only from the Gulf of Panama. I have found that both species occupy almost the whole of the tropical-subtropical region of the eastern Pacific. This region extends from the cape region of Baja California to about 6°S off northern Peru near Point Aguja (Ekman, 1953). Ekman includes in this warm-water region the Gulf of California and the Galapagos Islands and regards the area from 3° to 6°S as possibly a transitional zone containing a subtropical fauna. Rosenblatt (1967) considers the southern limit of the tropical region to be at Cabo Blanco, Peru, about 4°S.

P. snyderi occurs as far north as the upper Gulf of California, and Punta San Juanico (about 26°N) on the lower outer coast of Baja California, conforming to C. L. Hubbs' (1960) statement that tropical elements persist much farther north in the Gulf than on the outer coast. This species is not known southward beyond the Gulf of Panama, but it is a rarely-collected species and probably will be found as far south as the Gulf of Guayaquil, Ecuador (about 3°S).

P. medius ranges from the vicinity of Paita, Peru (about 5°S), northward to Bahía Topolobampo (about 25°N) in the southern Gulf of California, thus occupying almost all of the warm-water region.

One uncertain record exists for the Galapagos Islands.

P. simillimus occupies essentially the warm temperate region of the eastern Pacific, but ranges into so-called transitional areas northward and southward. This species occurs from Bahía Magdalena (about 25°N) on the outer coast of Baja California to the southern coast of British Columbia (about 48°N). This species occurs mainly in the Californian Province which extends to about 48°N (Schenck and Keen, 1936). *P. simillimus* is most abundant in an area corresponding closely to the warm temperate San Diegan division of C. L. Hubbs (1960). It is less abundant in the cool temperate division (Montereyan of Hubbs), and even less abundant in the somewhat transitional region between 42°N and 48°N of Schenck and Keen (1936).

In general, the species of *Peprilus* occupy broadly the major faunal regions of the continental shelf. Especially in the warm-water region of the eastern Pacific, the species cross the faunal subregions which have been established mainly from the study of generally small, more restricted fishes of rocky shores such as clinids, gobiesocids, tripterygiids, and chaenopsids (C. Hubbs, 1952; Briggs, 1955; Springer, 1958; Rosenblatt, 1959; and Stephens, 1963).

Degree of divergence in allopatric and sympatric sets of species. Sympatry over an extensive area occurs only in three situations among the seven species of *Peprilus*. The group is somewhat reminiscent of the superspecies concept, superspecies being defined (Mayr, 1963) as a monophyletic group of entirely or essentially allopatric species that are morphologically too distinct to be included in a single species and, thus, that reproductive isolation between them can be assumed.

The genus has a rather narrow ecological diversity. Therefore, it is important to know which species are sympatric and how niche separation is effected in sympatric situations.

TABLE 26. VALUES OF COEFFICIENT OF DIFFERENCE (C.D.) FOR THREE PAIRS OF SPECIES OF *PEPRILUS*.

CHARACTER (Morphometrics in thousandths of SL)	*burti triacanthus* allopatric	*triacanthus simillimus* allopatric	*triacanthus paru* sympatric
Head length	0.27	0.08	0.31
Snout length	0.12	0.08	0.58
Eye diameter	0.46	0.46	0.56
Upper jaw length	0.22	0.56	0.05
Interorbital width	0.28	0.22	1.01
Pectoral fin length	0.25	0.40	1.06
Predorsal distance I	0.21	0.23	0.81
Predorsal distance II	0.18	0.26	0.63
Preanal distance	0.31	0.10	0.53
Body depth	1.11	0.04	2.34
Caudal peduncle depth	0.34	0.43	1.45
Dorsal rays	0.22	0.15	0.43
Anal rays	0.22	0.28	0.03
Pectoral rays	0.44	0.20	0.62
Gill rakers	0.26	0.05	1.35
Vertebrae	2.39	1.72	2.50
Sum of C.D.	7.28	5.26	14.26
Sum of C.D.*	4.89	3.54	11.76

* Excluding vertebrae.

Coefficients of difference (C.D.) for morphometric and meristic characters were calculated for three pairs of species. The individual and summed C.D. values for each of the either allopatric or sympatric pairs are given in Table 26. The value is obtained by dividing the difference in the means of a character of two populations by the sum of their standard deviations (Mayr, Linsley, and Usinger, 1953: Chapter 7). A value of C.D. which these authors consider to be the conventional level for designating subspecies is 1.28 or above. The method is used here not for subspecific distinctions, but to show that generally in the genus *Peprilus* the diverse sets of species are sympatric and the similar ones allopatric.

P. snyderi and *P. medius* are sympatric throughout much of the warm-water region of the eastern Pacific. They have been taken in the same hauls and are members of different species groups. *P. snyderi* is the more rarely collected of the two species, and although the data are meager, it seems to be a more vagile fish and one more frequently in deep water than *P. medius.* Collections of the latter species are mostly from shallow coastal areas and bays.

P. snyderi and *P. simillimus,* two quite similar species (Table 21), are sympatric in a small region on the outer coast of Baja California; however, there is only one record of *P. snyderi* from this region. I believe that the two species very rarely come in contact, especially during the breeding season. *P. snyderi* probably breeds only farther south along the Mexican coast. *P. simillimus* replaces the tropical *P. snyderi* northward in temperate waters.

One record exists for *P. snyderi* in the upper Gulf of California where it would come in contact with the considerably dissimilar *P. ovatus. P. snyderi* is apparently quite rare in this region, also.

P. snyderi differs noticeably from *P. medius* and *P. ovatus,* but less so from *P. simillimus* (Figs. 2–6; Table 21). The differences seem to reflect the acquisitions associated with the trend toward a deep, short body in *P. ovatus* and *P. medius,* and include a larger eye, deeper body, slightly longer pectoral fin, and deeper caudal peduncle. These differences may be correlated with an existence in a shallow, essentially inshore habitat. The longer pectoral fin, shorter body, and deeper caudal peduncle seem suited for short-distance, nonmigratory swimming, and the larger eye an adaptation for living continuously in highly productive, but less transparent inshore waters.

In the Atlantic *P. paru* is sympatric with *P. burti* and with *P. triacanthus,* except in the northern portion of the range of the latter. *P. paru* best exemplifies the trend within the genus toward a short, deep body (Table 21; Figs. 2–6). It is a shallow-water, inshore species while *P. triacanthus* and *P. burti* seasonally migrate between inshore and offshore waters and are more regularly in deeper water.

The premaxillary teeth of *P. triacanthus* and *P. burti* each have three small cusps (Fig. 33b) while those of *P. paru* and the rest of the species are generally simple and pointed (Fig. 33a). The teeth of the lower jaw of all the species of *Peprilus* are multicusped but the cusp pattern in *P. burti* and *P. triacanthus* is slightly different. The significance of these differences in the teeth is as yet unknown; however, they may indicate a slight difference or segregation in food habits between say, *P. paru* and *P. triacanthus.* Mouth size (Fig. 4) and, apparently, food habits are similar among the species.

The above comparisons show that sympatry involves the more diverse sets of species, whereas the sets or pairs of species which are very similar tend to parallel one another in different oceans or to replace one another in adjacent faunal regions with perhaps a small area of sympatry or none at all. Niche separation is to a considerable degree effected spatially, i.e., one species in shallow water and a second ranging over a more extensive area of the shelf and generally in deeper water. There may be some shifts in food habits among sympatric forms or some type of resource subdivision, although no differences in diet among species have been discovered. This apparent similarity in food habits further suggests that spatial arrangement and ecological displacement are important in niche separation.

The nature of speciation in the genus Peprilus. Most of the differentiation and speciation in the genus seems to have taken place since the emergence of the Central American land bridge in the Pliocene. Before the emergence, the tropical faunas of the eastern Pacific-western Atlantic were apparently continuous and homogeneous. Rates of evolution in the group are difficult to estimate since there is substantial difference of opinion as to the time in the Pliocene when the land bridge was completely formed. Briggs (1967), in following Simpson's (1950) statement that the Isthmus of Panama made its last emergence in the latest Pliocene or earliest Pleistocene, estimates an age of one and one-half million years for the Central American barrier. Schuchert (1935) and Durham and Allison (1960) consider the time of emergence as the early Pliocene (or perhaps the late Miocene according to a reference of the latter authors). With the length of Pliocene as approximately ten million years (Kummel, 1961), a discrepancy of perhaps six to eight million years exists for the time of isolation of the Atlantic and Pacific faunas, depending upon whether one considers the early Pliocene or the late Pliocene as the date of closing of the seaway. Ira Rubinoff (personal communication) favors a period of three to four million years as the length of time since the effective separation of the Atlantic and Pacific shore faunas.

In general, the isolation of the two faunas has resulted in divergence to the species level, which may indicate the later closure of the seaway since the average age of a species might cautiously be considered to range from 100,000 to a few million years (Rensch, 1959). Rosenblatt (1967) finds that the shorefish faunas of the two sides of the Americas exhibit profound similarities on the familial, subfamilial, and generic levels, but that few species are common to both coasts. According to Briggs (1967), only about 12 of the approximately 1000 fish species along the tropical American coasts are still identical, making the Central American barrier 99 per cent effective. Members of the genus *Peprilus* conform to this pattern in that the genus is found on both coasts, but none of the species occur on both sides.

The members of the genus have considerably higher vagility and a greater ability for genetic interchange over a broad geographic region than do a number of other coastal fishes, particularly those of rocky shores. The fishes of this genus possess considerable ability not only for active dispersal but for passive disperal as well via the planktonic stages of eggs and larvae. They are of medium size (smaller than 300 mm in length) and have a life span of several years (at least three or four years), characteristics which should contribute to the maintenance of genetic interchange and a certain homogeneity within a particular species. In contrast, the controlling factors in the distribution of fishes of rocky littoral areas are more restrictive and localizing in nature. Rosenblatt (1963) states that fishes of rocky shores and coral areas are usually small, short-lived (perhaps one or two years), often territorial, and either have a short pelagic larval period or are even viviparous as is characteristic of a number of families of rocky littoral zones. He reasons that these factors curtail gene flow, frequently change the composition of the gene pool, and lead to differences in gene frequency either randomly or in response to local conditions. Such a population structure is favorable for the fragmentation of a species and the evolution of new species. The genus *Peprilus* and similar genera with wide-ranging coastal species are usually much less speciose than genera of rocky shores, and usually traverse the zoogeographic subregions occupied by fishes of rocky littoral areas.

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SUMMARY

A revision is presented of the genus *Peprilus*, one of the three genera of the family Stromateidae. The nominal genera *Poronotus* and *Palometa* are placed in the synonymy of *Peprilus*. Seven species are recognized in the genus. *P. ovatus* is described as a new species and is apparently restricted to the northern Gulf of California. *P. medius* and *P. palometa* are synonyms, and the former is the valid name. *P. alepidotus* is treated as a synonym of *P. paru*. Accounts of each species consist of a synonymy, diagnosis, description, distribution, the geographic variation, and the ontogenetic change.

The genus *Peprilus* occurs in tropical and temperate waters along the coasts of North, Central, and northern South America. Four species, *P. medius, P. ovatus, P. simillimus,* and *P. snyderi,* are distributed along the Pacific Coast, and three, *P. triacanthus, P. burti,* and *P. paru,* along the Atlantic Coast.

Several aspects of functional morphology are considered. The vertebral column, skull, and pectoral fins appear to ossify earlier than the caudal skeleton and median fins, a sequence interpreted as being correlated with an early planktonic life followed by an independent nektonic existence. Vertebral number is relatively constant within a species and is considered to be of possible selective value in maintaining a certain body form. The absence of pelvic fins, the long pectoral fins which are used extensively for propulsion in adult fishes, and the compressed body may all be correlated with the continuous swimming habit of these fishes, especially those larger than 100 mm SL. An hypothesis is presented that the swimbladder is of hydrostatic advantage to juvenile fishes which hover under jellyfish medusae and that it becomes nonfunctional in larger fishes which swim continuously. The scales are highly deciduous, and the skin is underlain by an extensive canal system, the function of which is unknown. The alimentary canal is composed of a small mouth with nipping teeth, a toothed, muscular pharyngeal sac, a U-shaped stomach, numerous pyloric caeca, and a long intestine. The food is shredded in the pharyngeal sac, and the great absorptive area of the caeca and intestine probably allows for maximum utilization of jellyfish and other food items.

Considerations of life history and ecology are generally of four species – *P. triacanthus, P. burti, P. paru,* and *P. simillimus.* Spawning occurs in the pelagic surface layers at varying distances from shore. The eggs and larvae are planktonic, the latter becoming capable of independent locomotion at a size of about 10 to 15 mm SL. The species occur in a wide range of salinity and variously inhabit all depths over the continental shelf and generally over a sand or mud bottom. The genus is essentially tropical and warm temperate, with only two species, *P. triacanthus* and *P. simillimus,* reaching cooler waters. Seasonal movements appear to be most pronounced in *P. triacanthus,* the species occurring most abundantly in temperate regions. Fishes smaller than 100 mm SL associate with jellyfish medusae of several

genera. This association is apparently important during the early critical growth phases of the fishes. *Peprilus* is a low-level carnivore; jellyfish medusae seem to be an important element in the diet, especially of juveniles. Other food items include a variety of small crustaceans, polychaete worms, and small fishes. Members of the genus are evidently significant forage fishes for a number of larger fishes, some of which are of great commercial importance. The economically important species of *Peprilus* are generally taken commercially in a region much smaller than the total range of the species, and this seems to reflect the pattern of migration and center of abundance of the particular species.

Disruption of the Tethys Sea in the Miocene apparently facilitated the segregation of the early members of the family Stromateidae and led to the evolution of the three extant and essentially allopatric genera. The formation of the Central American land bridge in the Pliocene, the emergence and submergence of land areas associated with the Pleistocene glacial and interglacial periods, and the prevailing current systems all appear to have been important in producing the current level of differentiation and speciation in the genus.

The elongate *P. snyderi* is considered to be the most primitive type and the deep-bodied *P. paru* the most highly derived form in the genus. The Camin-Sokal method for deducing relationships of contemporaneous species is used to reconstruct a dendrogram of species relationships. Two somewhat subtle species groups are recognized in the genus, and each group is represented on both sides of the Central American isthmus. Character displacement is invoked as a possible mechanism to explain the existence of two apparently distinct populations of *P. triacanthus* in the Atlantic off the southeastern coast of the United States.

The distribution of the species of *Peprilus* appears to correspond generally to the major faunal provinces of the Atlantic Coast and the Pacific Coast of the Americas. The species generally traverse the zoogeographic subdivisions established from the study of small fishes inhabiting rocky shores. Sympatry involves the more diverse species, and the similar or closely related species tend to parallel one another in different oceans or displace one another latitudinally along a continuous coastline. Niche separation seems to be produced largely by spatial arrangement and ecological displacement.

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